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THE EFFECT OF FOOD AVAILABILITY ON BLACK-BILLED MAGPIE REPRODUCTION

by

© WESLEY MICHAEL HOCHACHKA

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

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Date 9 September 1985

Abstract

The chief objective of this study was to determine how food availability influenced black-billed magpie (*Pica pica*) reproduction. Also examined were the relationships of fledging success with parental size, date of clutch initiation, clutch size, egg size, and egg composition. The effect of food availability was examined with food supplementation experiments, in which provisioning with supplemental food was begun on a territory either before or after eggs were laid. By starting food supplementation at different stages of the nesting cycle, I was able to determine that natural food was in short supply before, but not after eggs hatched. Supplemental feeding advanced clutch initiation, affected egg composition, increased the number of fledglings produced from a nest, and tended to increase the likelihood of re-nesting if an initial nesting attempt failed. The main effect of supplemental feeding on egg composition was to increase the variability in egg composition (but not egg volume) within a nest. Parental size, egg volume, and clutch size all did not affect fledging success. Date of clutch initiation had a very weak effect on fledgling production. I conclude: (1.) that annual fledgling production is primarily influenced by environmental factors, among them food availability, (2.) that the period during which food supply was most near a critical level was at or before egg laying, and (3.) that poor food availability during this time may have affected egg quality or parental condition.

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As a student of ecology, I have come to accept the presence of complicated, and sometimes unexpected inter-relationship among events. I therefore feel duty-bound to acknowledge all who have ever interacted with me, who create the environment in which I developed, who shaped my views of the world, and who provided their support, guidance, aid, and patience while I nurtured this thesis. Their influence appears in the form this thesis took.

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Table of Contents

Chapter	Page
Abstract	iv
Acknowledgements	v
I. INTRODUCTION	1
RATIONALE	2
THE STUDY ANIMAL	2
THESIS ORGANIZATION	3
SEMANTICS	3
LITERATURE CITED	6
II. REPRODUCTIVE BIOLOGY OF BLACK-BILLED MAGPIES IN THE CITY OF EDMONTON, ALBERTA	8
INTRODUCTION	9
METHODS	10
RESULTS	14
Habitat and Year Comparisons	14
Comparisons Among Territories and Breeding Adults	20
DISCUSSION	32
Inter-habitat Variation in Reproduction	32
Territory and Parental Quality	34
CONCLUSIONS	38
LITERATURE CITED	39
III. THE EFFECT OF SUPPLEMENTAL FEEDING ON THE REPRODUCTIVE OUTPUT OF BLACK-BILLED MAGPIES IN EDMONTON, ALBERTA	44
INTRODUCTION	45
METHODS AND RATIONALE	45
RESULTS	50
Food Use	50
Reproductive Parameters	50
DISCUSSION	53
Methodology	53
Reproductive Parameters	58

Conclusions 62
LITERATURE CITED 63
IV. THE COMPOSITION OF BLACK-BILLED MAGPIE EGGS 66
INTRODUCTION 67
METHODS 67
RESULTS 69
Egg Size Variation 69
Variation in Egg Composition Among Clutches 69
Variation in Egg Composition Within Clutches 77
DISCUSSION 80
Comparison With Other Studies 80
Variation in Magpie Egg Composition 82
Conclusions 85
LITERATURE CITED 87
V. CONCLUDING DISCUSSION 89
LITERATURE CITED 96

List of Tables

Table		Page
II-1	Laying dates among years and habitats	15
II-2	Clutch size among years and habitats	16
II-3	Rate of nest failure	18
II-4	Fledging success among years and habitats	19
III-1	Nutrient content of the supplemental food	46
III-2	Effect of supplemental food on laying date	52
III-3	Fledging success with post-laying food supplementation	55
III-4	Fledging success with pre-laying food supplementation	56
IV-1	Variation in egg size within and among clutches	70
IV-2	Effect of supplemental feeding on egg size	71
IV-3	Component masses of eggs from different sources	72
IV-4	Regressions of egg size on egg component masses	74
IV-5	Within clutch variation in egg composition	78
IV-6	Effect of supplemental feeding on intra-clutch egg composition	79
IV-7	Magpie eggs in England and Canada	81

List of Figures

Figure		Page
II-1	Location of study areas	11
II-2	Relationship between egg and clutch sizes	22
II-3	Relationship between egg size and fledging success	23
II-4	Clutch size on territories in successive years	25
II-5	Fledging success on territories in successive years	26
II-6	Female size and clutch size	28
II-7	Male size and clutch size	29
II-8	Female size and fledging success	30
II-9	Male size and fledging success	31
III-1	Availability of supplemental food to black-billed magpies	48
III-2	Rate of disappearance of supplemental food	51
IV-1	Egg size and albumin mass of black-billed magpie eggs	75
IV-2	Egg size and water content of black-billed magpie eggs	76

Chapter I

INTRODUCTION

RATIONALE

Heritable variation among individuals of a species is the base upon which natural selection acts. However, recent work (James 1983) indicates that some avian morphological traits, previously assumed to be heritable, are partially under environmental control. Birds, translocated as embryos to a new environment resemble members of the local population as well as the population from which they came. This phenomenon may also act on a local scale, confounding attempts to determine heritability of traits using measures of repeatability. For example, if a female nests in a similar environment each year, genetic and environmental influence on such attributes as clutch size could be indistinguishable.

Separating intrinsic (genetic) and extrinsic (environmental) influences on reproduction is important as reproductive parameters are used to estimate the (genetic) fitness of animals (Mock 1983). Evolutionary arguments must consider the degree to which fitness is actually under genetic control.

This thesis describes work that addresses this problem. In particular, I have attempted to determine the role of food availability (an environmental factor) in influencing reproductive success. This does not imply that I favour the importance of environmental influences, but merely indicates that data relevant to questions about intrinsic differences were not readily obtainable. In this thesis I show the stage(s) in the reproductive cycle at which environmental influences can affect reproductive success.

In the analyses that follow, the data have been considered at a number of levels. The different spatial scales used were: (1.) among disjunct groups of nests, (2.) among nests within a group, (3.) and among young within a nest. Temporal variation has been considered both among and within years. Variation in reproductive parameters occurs at each of these levels, making analyses at various levels useful for different purposes.

THE STUDY ANIMAL

The animal used in this study was the black-billed magpie (*Pica pica hudsonia*), the North American sub-species of a bird which has a nearly holarctic distribution, being absent only from parts of central Asia and from eastern North America (Goodwin 1976).

In Alberta, the magpie apparently has expanded its range northward in in this century (*e.g.* Farley 1932), and is now a common resident in the city of Edmonton, where this study was undertaken.

The magpie breeds at relatively high densities (roughly 30 breeding pairs per square kilometre on the University of Alberta campus), nests being large, easily locatable structures. Magpies are also omnivorous (Linsdale 1937, Goodwin 1976) which makes them amenable to experimental supplementation of their food supply (Högstedt 1981a, Chapter III), and consequently good subjects with which to examine the effects of food availability on reproduction. Also invaluable to this study was previous research on magpies in the city of Edmonton (Scharf 1985), other parts of North America (*e.g.* Linsdale 1937), and in Europe (*e.g.* Baeyens 1979, Högstedt 1981a, Tatner 1982).

THESIS ORGANIZATION

The body of this thesis is in Chapters II, III, and IV. Chapter II is a description of magpie reproduction in Edmonton; this chapter provides background information for the experimental work in Chapters III and IV. Results of a food supplementation experiment are described in Chapter III. Chapter IV provides data on the variation in composition of magpie eggs within and between nests.

SEMANTICS

Three terms which are frequently used in this thesis, need definition. The terms are fledging success (measured as the number of young banded at a given nest), fitness, and quality. I use fledging success as the number of fledglings produced from a nest, but only those nests where at least one chick was fledged. Thus, I have differentiated between nesting attempts which fledged no young, and those from which fledglings were produced. The rationale is that partial loss of nestlings may represent an adaptive adjustment to that number which the parents (or the territory) can support (*e.g.* Ricklefs 1965); total nest failure may represent other phenomena such as nest predation (*e.g.* Yom-Tov 1974) or catastrophe such as the nest being dislodged from the tree. Although

partial and total loss of eggs / young may not always be due to separate causes, I feel that this distinction is still useful.

Fitness is a concept central to evolutionary biology. The fitness of as organism is the representation of its genetic material in subsequent generations. Thus both direct descendents (*e.g.* offspring, grand-offspring), and less direct descendents (*e.g.* nephews, nieces) contribute to fitness. As the descendents most closely related to parents are their offspring, the lifetime reproductive output of an organism will make up a large measure of the parents' genetic contribution to the next generation. Thus, in this thesis, the terms "fitness" and "lifetime reproductive output" will be used interchangably.

Throughout this thesis the word "quality" will frequently appear. In the ecological literature "quality" has tended to remain an undefined concept. This is because fitness is ultimately the only relavent measure of success of individuals. In this thesis, the word quality will be used in the following way: a "high quality bird" is one which has relatively high annual reproductive output in the absence of environmental variation, and a "high quality territory" will impart high annual reproduction on breeding birds in the absence of intrinsic differences.

In an ecological context, any measure of quality should involve fitness, which is the representation of an individuals genetic information in future generations. The measures of quality I have used are annual reproductive rates (clutch size and fledging success), whereas fitness measures lifetime reproductive output. As measures of intrinsic differences in quality, annual reproductive output may be inadequate; in some species high reproductive output in a given year may affect the probability of survival to the next year (*e.g.* Charnov and Krebs 1974, Askenmo 1977, Nur 1984). Using my definition of quality, an adult magpie would be considered of high quality if it produced a large number of young in one year, but the stress of this high reproductive rate could actually result in the bird dying (decreasing the number of years it is in the reproductive population and possibly its lifetime reproduction (fitness)). I do not know whether annual reproductive rates are correlated (either negatively or positively) with lifetime reproduction for magpies in Edmonton. However, Högstedt (1981b) provides evidence that magpie survival is, over a bird's first four breeding seasons, positively correlated with reproductive rate.

Ideally, one should be able to measure territory quality directly as the environmental factor(s) which influence reproduction. However, as the critical environmental parameters are unknown, the influence of environment on reproduction must be inferred from data on reproductive rates. It should be less problematic to equate territory quality with fitness, than parental quality with fitness. If a territory is of high quality, allowing magpies to raise relatively many young in a given year, the greater reproduction should be due to higher use of environmental resources, not parental (survival compromising) resources. Higher reproduction because of high territory quality should represent a real increase in fitness, as parental survival is not compromised. Admittedly, a more accurate measure of relative territory quality would be obtained by monitoring reproduction on territories over a number of years. In a crude way, this has been done for ruffed (*Bonasa umbellus*) (Boag 1976) and blue grouse (*Dendragapus obscurus*) (Lewis and Zwickel 1981), and for magpies in Denmark (Møller 1982). These measures were the proportions of years a territory was occupied; only presence or absence of reproduction was recorded for a given year. A more accurate measure would be to treat unoccupied territories (0 reproduction in a given year) on a continuum of production of 0, 1, 2, or more young in a year. These types of data are currently unavailable for magpies in Edmonton, and thus yearly measures of reproduction were used in an attempt to determine the effect of territory quality on reproduction.

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Chapter II

REPRODUCTIVE BIOLOGY OF BLACK-BILLED MAGPIES IN THE CITY OF EDMONTON, ALBERTA

INTRODUCTION

Ultimately, the fitness of an individual is determined by the extent its genetic information is represented in successive generations. Ecologists, however, cannot measure fitness at this basic level, and must assume that various indices of reproductive success are reasonable estimates of fitness (Mock 1983). Reproductive success can be estimated at different stages of the reproductive cycle (*e.g.* Howard 1979). For birds, it can be estimated as clutch size, number of young hatching, or number surviving to fledging or beyond. The later in the breeding cycle these estimates are made, the more accurate their reflection of fitness will be, because the measures will be closer to the time the young enter the breeding population.

At a proximal level reproductive success can be affected by both intrinsic and extrinsic factors. Intrinsically, clutch size is to some extent genetically controlled (Perrins and Jones 1974, Batt and Prince 1979, van Noordwijk *et al*. 1980). Extrinsically, variations in the availability of food in the environment (Högstedt 1981, Dijkstra *et al*. 1982, Scott and Birkhead 1983), or in foraging ability of the individual (Howe 1976, de Steven 1978, Högstedt 1980) could influence the amount of food a female finds (or is fed by her mate), affecting the nutritional condition of the female. Clutch size in birds can be influenced by the level of the nutrient reserves present in the female (Jones and Ward 1976, 1979, Fogden and Fogden 1979, Krapu 1981, McGillivray 1983), as could the ability of the female to aid in the feeding of the young. Hatchability of eggs may be influenced by some (as yet unidentified) intrinsic and extrinsic factors (Moss *et al*. 1981). Food availability may also limit the number of nestlings which survive to fledging (*e.g.* Klomp 1970, Bryant 1975, Högstedt 1981). Additionally, territory quality, aside from food availability, may affect egg and nestling survival through the proximity of nest predators (Baeyens 1981a), and the ability of dults to guard their nests against predators (Yom-Tov 1974, Spray 1978). Post-fledging survival can be influenced by factors in the nestling period; for example, fledging weight can be related to post-fledging survival (Perrins 1965, Nur 1984).

This chapter provides information on laying date, clutch size, and fledging success in an urban population of black-billed magpies in the city of Edmonton. The data are descriptive in nature, and serve mainly to provide background information necessary for

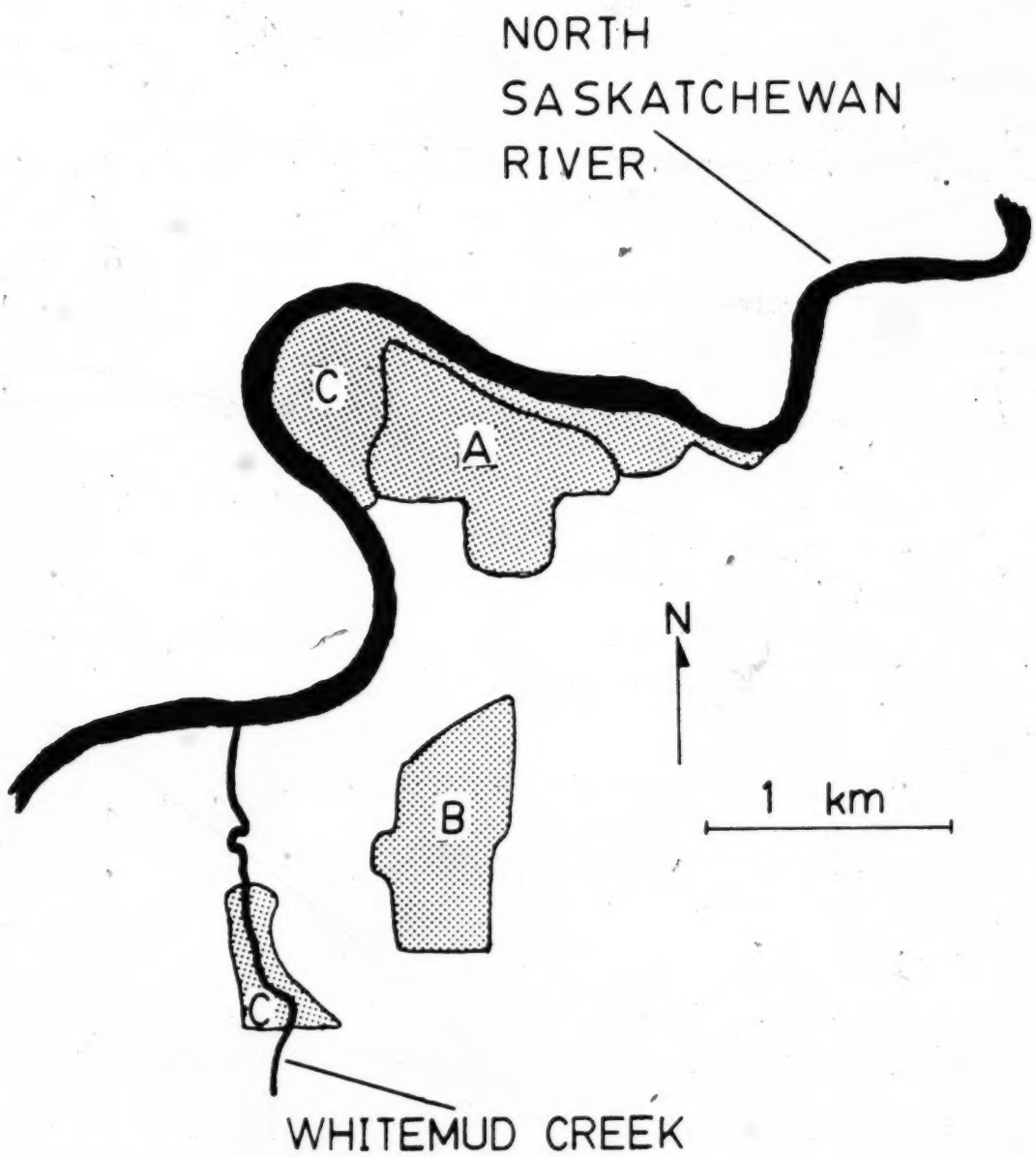
the analysis, interpretation and discussion of the experimental work in Chapters III and IV.

METHODS

This study was conducted during the summers of 1981-84 inclusive. Data were obtained in three areas which, for the rest of this thesis, will be termed the urban, farm, and river valley habitats (Figure II-1). The urban habitat, on and around the University of Alberta campus, has many mature coniferous and deciduous trees, lawns and gardens interspersed among its buildings. The farm habitat, on the University of Alberta experimental farm, contains pastures interspersed with patches of trees and shrubs. Cattle, sheep, swine, chickens, and turkeys are present on the farm. The third habitat, composed of parts of the valleys of Whitemud Creek and the North Saskatchewan River, is the most variable of the three, ranging from essentially pure stands of white spruce (*Picea glauca*), through mixed woods forests, to pure poplar (*Populus tremuloides* and *P. balsamifera*) forest. Additionally, there are municipal park areas with large lawns interspersed with plantings of trees (mostly spruce). River valley magpie territories were mainly in and adjacent to these park areas.

To my knowledge all occupied nests on the study area were found each year. Nest locations were recorded. For those nests which could be reached, clutch size was determined, and nestlings were marked with individual combinations of one metal and three coloured bands. Banding was usually done approximately 1 week before the young fledged, and the number of nestlings banded was taken to be the number that fledged. Young were not banded in only 7 of 196 nests in which fledging success was known. Over the first 3 years of the study, both clutch size and fledging success were recorded at 117 of 187 nests; logistics prevented recording of both data at 70 nests. On some territories in 1983 and 1984 supplemental food was provided, which influenced laying date and fledging success thereon (Chapter III). The data from food supplemented territories were not used in the analyses presented in this chapter. Further, in 1984 entire clutches of eggs were collected from 21 of 51 nests, for work described in Chapter IV. Renesting occurred in some cases, but data from second nesting attempts were also excluded from the analyses.

Figure II-1: Location of study areas in the city of Edmonton. "A" is the urban study habitat, "B" is the farm habitat, and "C" is the river valley habitat.



In 1984 eggs were measured at the nest (if the clutch was not collected) or in the lab. The length, and breadth at largest diameter were measured with dial calipers to 0.1 mm for each egg. The product of length and squared breadth (LB^2) was calculated as an index of egg volume. This measure is a reliable indicator of egg volume for birds (Hoyt 1979). For each nest, the mean egg volume index for all eggs was calculated. These mean values were used in the analysis of the effects of egg size on reproductive success.

At banding, nestlings were weighed to the nearest gram on a triple beam balance, and the depth of the bill at the front of the nares determined to 0.1 mm with dial calipers. Bill depth, unlike some other characters of nestling magpies, increases throughout the nestling period, making it useful in determining the age of nestlings. The growth of bill depth follows the logistic equation ($r^2=0.84$):

$$t = \frac{\ln(13.1/D - 1)}{-0.08} + 6.18$$

where t is the age in days and D, the bill depth in millimetres (Scharf, *unpubl.*). For each brood, an average nestling age at banding was estimated by solving the equation for age, using the mean bill depth of all young in a nest. Knowing nestling age, it was possible to estimate hatching date by back-dating. Nestling age was subtracted from the date of banding to give hatch date. An 18 day incubation period (Holyoak 1967, Johnson 1972, Alvarez and Reyma 1974) was subtracted from hatch date to give date of clutch completion. One egg is layed each day (Holyoak 1967, Tatner 1982, *pers. obs.*), with an apparent added gap of 1 day at some point in laying (Holyoak 1967); thus, clutch size plus 1 day is subtracted from date of clutch completion to yield date of clutch initiation.

In all years, from the time the first fledgling appeared until the end of August, the urban habitat was searched for banded fledglings. Fledgling sightings were made more sporadically after August. Identities and locations of marked fledglings were noted.

From 1982 to 1984 some territorial adult magpies were also colour banded. Some were caught over-winter in circular walk-in traps (Alsager *et al.* 1972). Most were caught during the breeding season using a live decoy magpie to attract territorial adults into an area where leg nooses were set (as described in Scharf 1985). Various measurements were taken on captured adult magpies: wing chord, wing breadth, tarsometatarsal length,

foot length (all to 1.0 mm), length of bill from gape to tip, length of bill from front of nares to tip, depth of bill at base of culmen, depth of bill at front of nares, width of bill at front of nares (all to 0.1 mm), and weight (in grams). Sex of captured magpies could be determined from these measurements (Scharf 1985), from presence or absence of brood patch if capture was during the breeding season, and from behavior of the birds during the course of the nesting cycle; for example, only female magpies incubate eggs and brood young (Goodwin 1976, p. 178).

The morphological measurements taken from adult magpies were reduced to a single variable. This size measure is the sum of all standardized linear measurements taken from that bird. The values for each variable were standardized as follows:

1. The mean and standard deviation were found for the entire sample.
2. The value measured for each bird was subtracted from the mean and divided by the standard deviation of the sample.

This procedure was done separately for data from males and females. After standardization, each variable had a mean of 0, and a standard deviation of 1. The standardized, and not the raw, data were summed in order to eliminate weighting of the variables by their magnitude.

Frequent disturbance of nesting magpies can lead to desertion during laying (T.R. Birkhead, *pers. comm.*), or decrease the number of fledglings produced (Trost and Hewitt 1981). Consequently, nests were checked five or fewer times during a breeding attempt. Thus, there are no data on laying or hatching sequence of eggs, hatchability of eggs, or the times at which nestling mortality occurred.

Data analyses were performed using BMDP procedures (Dixon *et al*. 1983) unless otherwise noted. The probability level at or below which results were termed significant was $P=0.05$. However, probabilities between $P=0.10$ and $P=0.05$ were noted as weakly suggestive of significance (Buckland 1982).

RESULTS

Habitat and Year Comparisons

Laying Date

Annual mean laying dates in the three habitats are presented in Table II-1. As variances were unequal among blocks, a two-way ANOVA could not be used to analyse the data. Separate yearly comparisons of laying date among habitats showed a significant difference only in 1984, when clutch initiation was significantly later on the urban than farm or river valley habitats. Inter-habitat differences approached significance in 1981. There was no consistent pattern of inter-habitat differences in laying date. Within habitats, there were significant differences in mean laying date among years, with 1984 having the earliest clutch initiations in two of the three habitats.

Clutch Size

Annual mean clutch sizes in the three habitats are given in Table II-2. Clutch size did not differ among either years or habitats, averaging 6.6 eggs. There was a weak trend for difference in clutch size among habitats, and the combined data for 4 years suggests that clutch size was higher in the farm and lower in the river valley habitat.

Egg Size

The size ($\bar{x}\pm$s.d. in cm^3) of eggs tended to vary among habitats (urban 16.56±1.73, n=9 clutches; farm 18.38±1.26, n=5 clutches; river valley 17.66±1.18, n=8 clutches), with differences only approaching significance (one-way ANOVA, P=0.09). The greatest difference was between small eggs on the urban habitat, and large eggs on the farm in 1984. Clutch initiation was also latest on the urban habitat and earliest on the farm in 1984 (Table II-1) which suggests a relationship between date of laying and egg size. However, such an apparent relationship may be an artifact of some other difference among habitats which is unrelated to laying date.

TABLE II-1: Dates of clutch initiation for black-billed magpies in urban, farm, and river valley habitats in the city of Edmonton for years 1981-1984. Laying dates are presented as $\bar{x}\pm$s.d. (n).

Year	Habitat			
	Urban	Farm	River valley	Probability[1]
1981	Apr. 17± 3 (16)	Apr. 25±12 (10)	Apr. 21± 5 (6)	P=0.10
1982	Apr. 27± 9 (20)	Apr. 27± 4 (10)	Apr. 27± 7 (12)	P=0.92
1983	Apr. 31±13 (9)	Apr. 24 (1)	Apr. 28± 1 (2)	P=0.37
1984[2]	Apr. 19± 5 (15)	Apr. 10± 2 (6)	Apr. 6± 6 (9)	P<0.001
Probability[1]	P<0.01	P<0.01	P<0.01	

[1]Levels of significance determined by separate Kruskal-Wallis tests on data within each year or habitat.

[2]Pair-wise comparisons among habitats (Conover 1980) revealed that laying was significantly later on the urban than farm or river valley habitats in 1984.

Table II-2: Clutch sizes of black-billed magpies nesting in urban, farm, and river valley habitats in the city of Edmonton for the years 1981-1984[1]. Values are presented as $\bar{x}$±s.d. (n).

	Habitat		
Year	Urban	Farm	River Valley
1981	7.0±1.2 (20)	6.4±1.8 (5)	6.0±1.8 (9)
1982	6.5±1.5 (30)	6.9±1.1 (10)	5.9±0.8 (11)
1983	6.5±1.3 (20)	6.3±1.2 (6)	6.4±1.0 (18)
1984	6.8±1.0 (22)	7.4±0.5 (5)	6.6±1.0 (14)
Total	6.7±1.3 (92)	6.8±1.2 (26)	6.3±1.2 (52)

[1]For a two-way ANOVA among years and habitats: year — P=0.27; habitat — P=0.10; year X habitat — P=0.61.

Fledging Success

The numbers of nestlings fledged from nests in the three habitats were compared. I considered loss of all nest contents (total failure) separately from partial loss of eggs / nestlings. Loss of all nest contents is a characteristic of predation (G. Högstedt, *pers. comm.*; Yom-Tov 1974). Partial loss of eggs or nestlings may indicate unhatched eggs, or loss of nestlings through starvation (*e.g.* Ricklefs 1965, Howe 1976) or other causes.

The frequencies with which nesting attempts failed did not differ among habitats within a given year (Table II-3). Nor was there a significant difference in failure rate among years for any given habitat. A relatively constant proportion (31.2%) of nests produce no fledglings. For those nests which produced at least one fledgling, the mean number of fledglings did differ among habitats (Table II-4). As no year-to-year differences were found, the data were combined over years in an *a posteriori* Newman-Keuls test, which showed that farm habitat nests produced more fledglings ($\bar{x}$=4.6) than either urban ($\bar{x}$=3.5) ($P<0.01$) or river valley ($\bar{x}$=3.5) ($P<0.025$) nests; production of fledglings in the urban and river valley habitats did not differ significantly ($P>0.50$). The collection of eggs in 1984 (Chapter IV) rendered 1984 data insufficient for inclusion in the two-way ANOVA. However, urban habitat data over the full 4 years of the study were sufficient to do a one-way ANOVA including some 1984 data; this ANOVA showed no significant difference in fledgling production in 1984 relative to the other years. Thus habitat, but not yearly differences existed in fledging success.

Summary

Mean laying date did vary among years, but not consistently among habitats. There was no year-to-year variation in clutch size, rate of nest failure or numbers of fledglings produced in nests. Habitat differences in clutch size and egg size (measured only in 1984) approached significance, with both clutches and eggs tending to be larger in the farm habitat than elsewhere. Nests on the farm produced significantly more fledglings than urban or river valley nests.

Table II-3: Number of nesting attempts that either successfully fledged at least one nestling, or failed to produce any young.

	Urban		Farm		River Valley		
Year	Fledged	Failed	Fledged	Failed	Fledged	Failed	Probability[1]
1981	19	13	11	2	7	4	$P>0.10$
1982	23	15	11	4	15	12	$P>0.50$
1983	21	3	7	1	11	7	$P>0.25$
1984	23	6					
Probability[1]	$P>0.10$		$P>0.90$		$P>0.95$		

[1]Probabilities determined by separate G-tests, comparing numbers of sucessful and unsuccessful nests.

Table II-4: Numbers [$\bar{x}$±s.d. (n)] of fledglings produced per nest in urban, farm, and river valley habitats, 1981-1984[1]. Data were available in 1984 only from the urban habitat. Data are from nests at which at least one fledgling was produced.

Year	Habitat		
	Urban[2]	Farm	River Valley
1981	3.8±1.8 (19)	4.2±1.6 (12)	4.1±1.7 (7)
1982	3.7±1.9 (18)	5.2±1.5 (11)	3.5±1.6 (15)
1983	2.8±1.4 (13)	4.0±2.0 (3)	2.6±1.8 (5)
1984	3.8±1.7 (20)		

[1]Based on a two-way ANOVA among years (1981-1983) and habitats: year — P=0.17; habitat — P=0.04; year X habitat — P=0.46.

[2]Based on a one-way ANOVA among years (1981-1984) in the urban habitat: P=0.32.

Comparisons Among Territories and Breeding Adults

Laying Date, Clutch Size, and Fledging Success

The previous section established that differences in magpie nesting success existed among nesting areas of different character. Although there was only a tendency for larger clutches to be produced on the farm habitat, fledging success was significantly higher there. Thus, even if clutch size influenced inter-habitat differences in fledging success, some additional factor(s) must be involved. To determine the strengths of the relationships between laying date, clutch size, and fledging success, comparisons were made of reproduction among individual nests. Potential, independent relationships among these variables were tested using correlations. A simple correlation was performed between date of clutch initiation and clutch size. However, as fledging success could be affected by both laying date and clutch size, it was necessary to use partial correlations in order to remove the effect of clutch size on fledging success when correlating date of clutch initiation and fledging success, and likewise, to remove the effect of laying date on the clutch size—fledging success correlation. For partial correlations, data were from all nests where at least two of the three parameters were known (pair-wise deletion of cases with missing values). Data on fledging success came from those nests in which at least one fledgling was produced. Correlations were performed using SPSSX (SPSS Inc. 1983). Data were combined over all years and habitats to obtain a larger sample size for the analysis. In combining data from different habitats, I assumed that similar relationships existed among the variables in all three habitats. In combining data over all 4 years, year-to-year differences in clutch initiation date were removed, following a procedure used by Tatner (1982), by adding 7, 0, 3, and 9 days to each laying date in 1981 to 1984 respectively. This equalized the mean laying date of all years to April 27. This "correction" of laying dates carries the implicit assumption that changes in clutch size or fledging success over a season are relative to mean laying date of that year, not calendar date. It is recognized that this "correction" of laying dates may have had an inherent error in 1984, when mean laying dates differed among habitats (Table II-1). Nevertheless, application of this procedure to 1984 data would tend to make the results of the correlation analysis more conservative.

Fledging success was inversely correlated with date of clutch initiation (r=-0.23, *d.f.*=67, *P*=0.03). Clutch size also showed the same relationship with clutch initiation date (r=-0.23, *d.f.*=71, *P*=0.03), Clutch size and fledging success tended to be positively correlated (r=0.18, *d.f.*=67, *P*=0.07). None of the correlations was very strong, suggesting that both laying date, and clutch size have only a minor effect on the number of young which fledge from a nest.

Egg Size

In 1984 mean egg size was measured for a number of nests. Egg size and clutch size were not related (Figure II-2). For those nests where eggs were not collected, no relationship was found between egg size and subsequent fledging success in that nest (Figure II-3).

Territory Quality

The spatial distribution of magpie territories remained relatively constant from one year to the next. The median distance between nests on a territory in consecutive years was 15.5 m (range 0-104 m). By contrast, the median distance between nearest neighbour nests was 100 m (range 46-294 m). This difference is highly significant (Mann-Whitney U-test, *P*<0.001). The largest annual nest site shifts occurred in areas of very low nesting density, and only 6 of 54 nest sites shifted more than 75 m, on a given territory. Given the relative stability of magpie territories it was possible to determine whether some territories have consistently higher reproductive output than others. Consistent differences in reproductive success among territories could indicate differences in territory quality. Some magpies, however, will breed on the same territories in consecutive years, thus potentially confounding any environmental effects on reproduction with parental effects. Of marked breeding adults, 23 of 40 (57.5%) males and 14 of 22 (63%) females returned to the study area after nesting on it the previous year. However, only 14 of 40 (35%) males and 4 of 22 (18%) females returned to the same territory in consecutive years. Because of the high turnover of magpies on territories, consistent differences in reproductive rates among territories are likely to be due mainly to effects of territory quality.

Figure II-2: Relationship between mean egg size for a clutch (as represented by the egg volume index, LB^2) and clutch size.

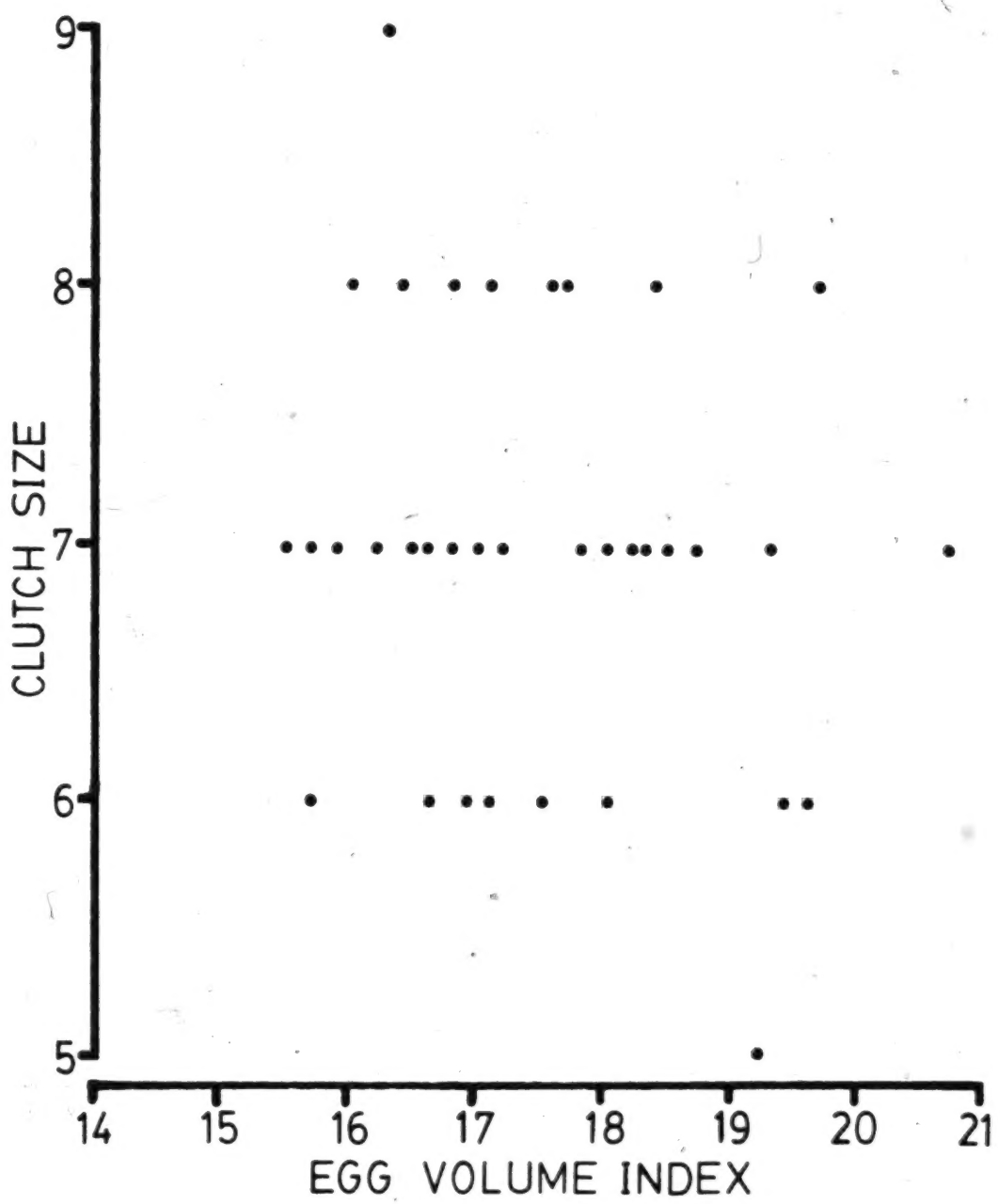
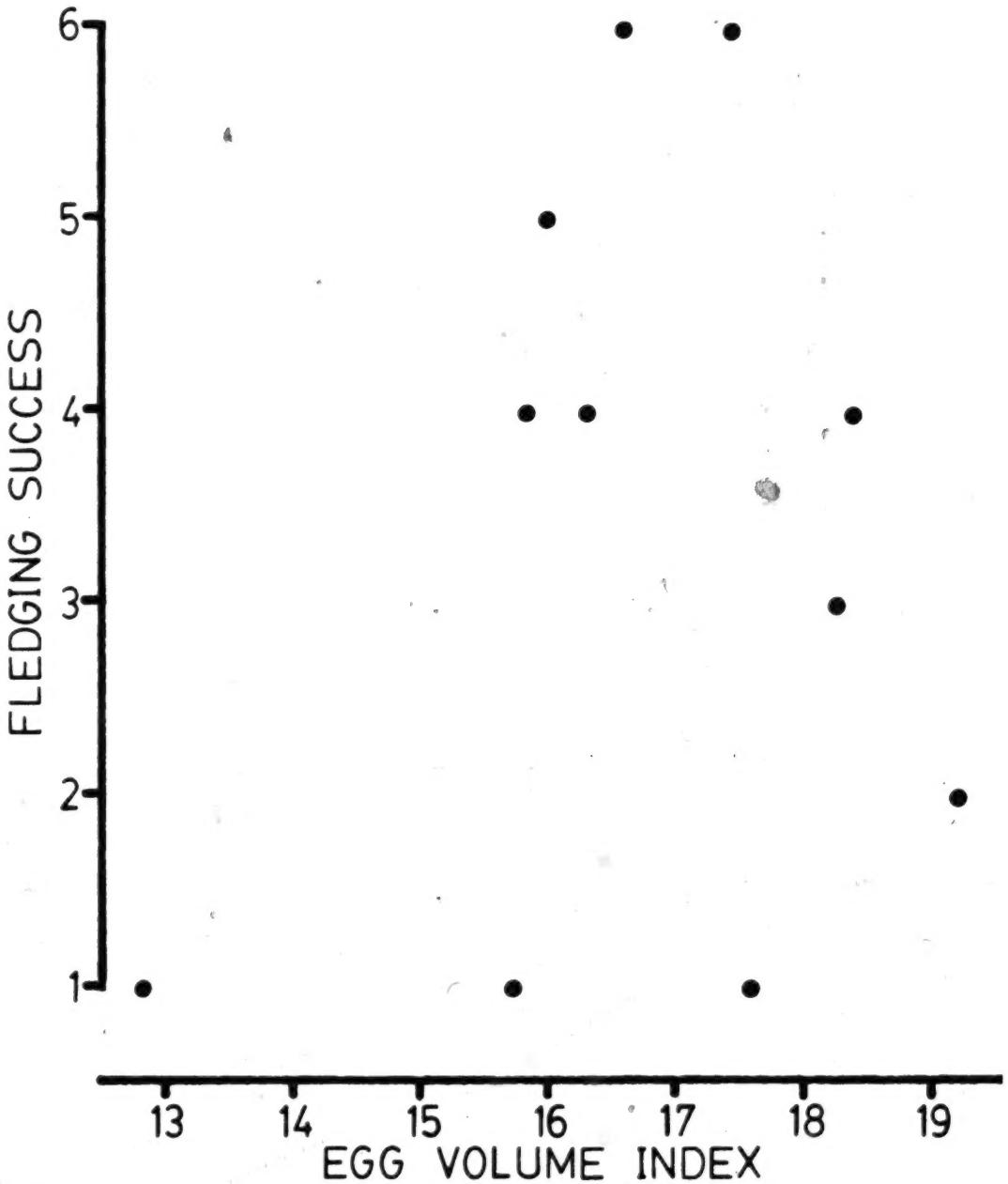


Figure II-3: Relationship between mean egg size for a clutch (as represented by the egg volume index, LB^2) and fledging success.



In comparing clutch size and fledging success from one year to the next, the data were standardized in order to eliminate the annual variation in these parameters. The data were standardized by subtraction of the yearly and habitat mean clutch size (or fledging success) from each datum taken from that year and habitat; thus, each datum represents the deviation of the reproductive output of that nest from the mean of that year and habitat. A comparison of clutch size on a given territory in year X with clutch size in year X+1 (Figure II-4) suggests no relationship. The same comparison using fledging success data showed a positive relationship (Figure II-5). In both figures, some territories are represented more than once, by data between different pairs of years. Numbers of fledglings, but not clutch size, was relatively consistent on a territory in two consecutive years.

Parental Characteristics

Little direct information is available on parental influences on reproductive rates. Figures II-4 and II-5 show all cases where known males (no data are available for females) nested on the same territory in consecutive years. There were too few such cases to warrant comment. When marked males changed territories between years, the clutch sizes of females on these territories were not correlated ($r=-0.82$, $P<0.20$, $n=4$), but fledging success tended to be positively correlated ($r=0.73$, $0.10>P>0.05$, $n=6$) between years. When females changed territories, clutch sizes on the two territories were uncorrelated ($r=0.09$, $P>0.50$, $n=4$). No data exist for fledging success of females which change territories. Thus, the meager existing evidence suggests that parental quality of the male may play a role in determining reproductive success. However, no conclusions should be drawn until larger samples are obtained.

I also looked for morphological correlates of reproductive success. The parental characteristics examined, relative to reproductive output, were size and shape of the territorial male and female. The descriptors of size used were the linear combinations of the measurements taken of adult body dimensions. The rationale for considering males, as well as females, is that aspects of male behavior could be correlated with morphology. For example, male dominance is positively correlated with size (Scharf 1985), and, if dominant males can acquire better territories (Smith 1976, Reese and Kadlec 1984), this

Figure II-4: Relationship between clutch size on a given territory in years X and X+1. Clutch size is measured as the difference between the observed clutch size, and mean clutch size for that year and habitat (*e.g.* -2 indicates that a clutch was 2 eggs smaller than the mean for that year and habitat). Known re-occupancy of the same territory in successive years by a marked male is denoted by ♂.

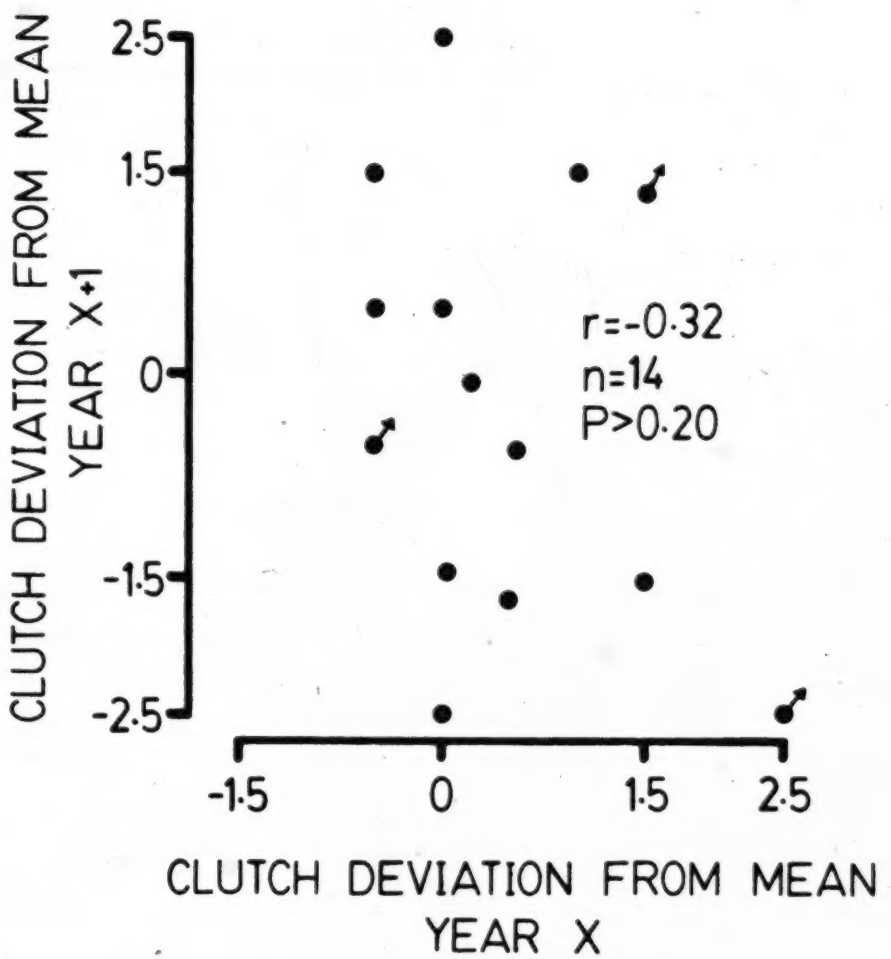
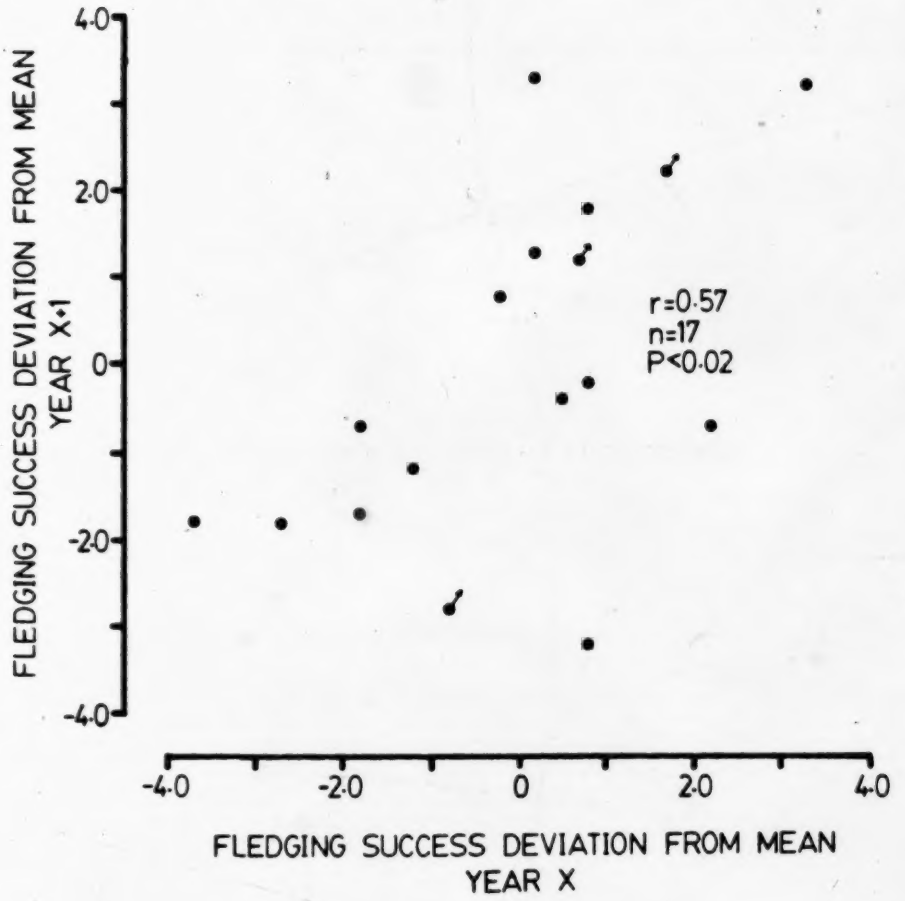


Figure II-5: Relationship between fledging success on a given territory in years X and X+1. Fledging success is measured as the difference between observed fledging success, and mean fledging success for that year and habitat (*e.g.* -2 indicates that fledging success in a nest was 2 young lower than average for that year and habitat). Known re-occupancy of the same territory in successive years by a marked male is denoted by ♂.



could be reflected in higher reproductive success. Female and male size were plotted against clutch size (Figures II-6 and II-7) and fledging success (Figures II-8 and II-9). None of the relationships was significant, although there is a suggestion that clutch size may increase with an increase in female size (Figure II-6). Female, but not male, morphology may influence clutch size, but neither showed any relationship with fledging success.

Post-fledging

Observations of post-fledging magpies can be used to determine rate of disappearance of fledglings from the study area. In this way a combination of mortality and dispersal can be estimated.

Within each nest in the urban habitat, the nestlings were ranked by weight at the time of banding. This weight hierarchy is assumed to carry through to fledging. Even before this time, weight hierarchies in magpie broods are relatively stable: for 5 nests (with 4 to 6 nestlings each), only 5 of 26 nestlings moved greater than one rank within their nest's weight hierarchy after a period of one week or more. Fledglings were also ranked according to the last date that they were sighted on the study area. Sightings may be two or more years after an individual fledged. For each nest, weight and last sighting ranks were correlated (Spearman's rank correlation). If no relationship exists between these variables, the collection of correlation coefficients of all nests should be normally distributed with a mean of 0. This was tested with a *t*-test, comparing the mean correlation coefficient to an expected mean of 0, with the hypothesis tested being whether heavier fledglings remained on the study area longer, *i.e.* either survived better (*e.g.* Perrins 1965) or dispersed less than lighter siblings. The result ($\bar{x}$=0.16, t=1.416, n=42, $0.10>P>0.05$) suggests that there was a tendency for heavier siblings to remain longer on the study area.

Post-fledging sightings were also used to give some indication of whether laying date influenced the survival and/or dispersal rates of fledglings from a nest. A bird was classified as surviving and non-dispersing if it was known to be on the study area in March (spring) of the year after it fledged, or any time thereafter. These data were available for fledglings from the 1981, 1982, and 1983 breeding seasons from nests in the urban habitat. The total number of fledglings produced was divided into equal early and late groups, the dividing line being the date of hatching of the median fledgling, when

Figure II-6: Relationship between clutch size (averaged, if more than one datum was available for a given female) and female size. Size was measured as the sum of standardized measures of body dimensions (see text for explaination of calculation of body size).

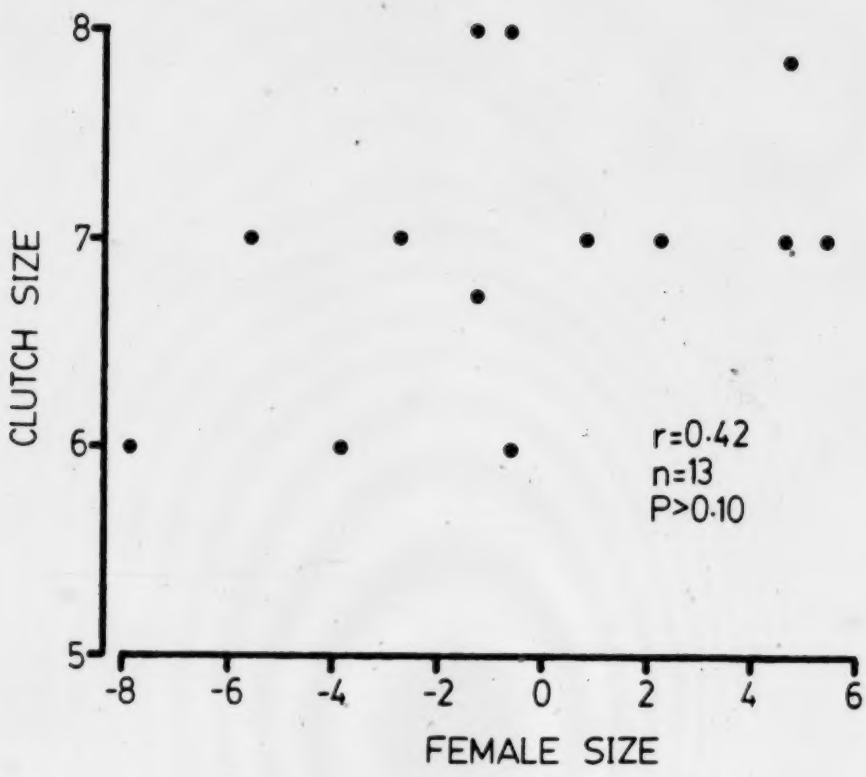


Figure II-7: Relationship between clutch size (averaged, if more than one datum was available for a given male) and male size. Size was measured as the sum of standardized measures of body dimensions (see text for explaination of calculation of body size).

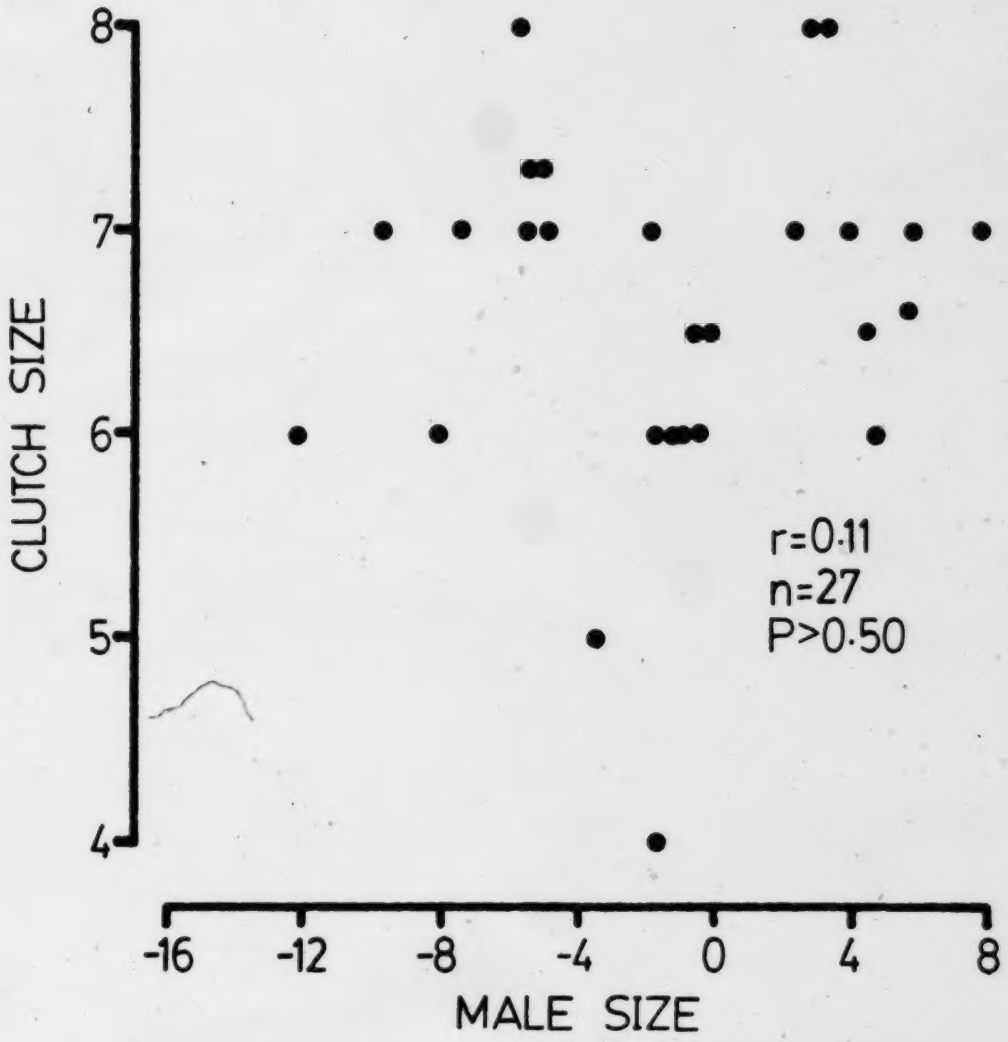


Figure II-8: Relationship between fledging success (averaged if more than one datum was available for a given female) and female size. Size was measured as the sum of standardized measures of body dimensions (see text for explaination of calculation of body size).

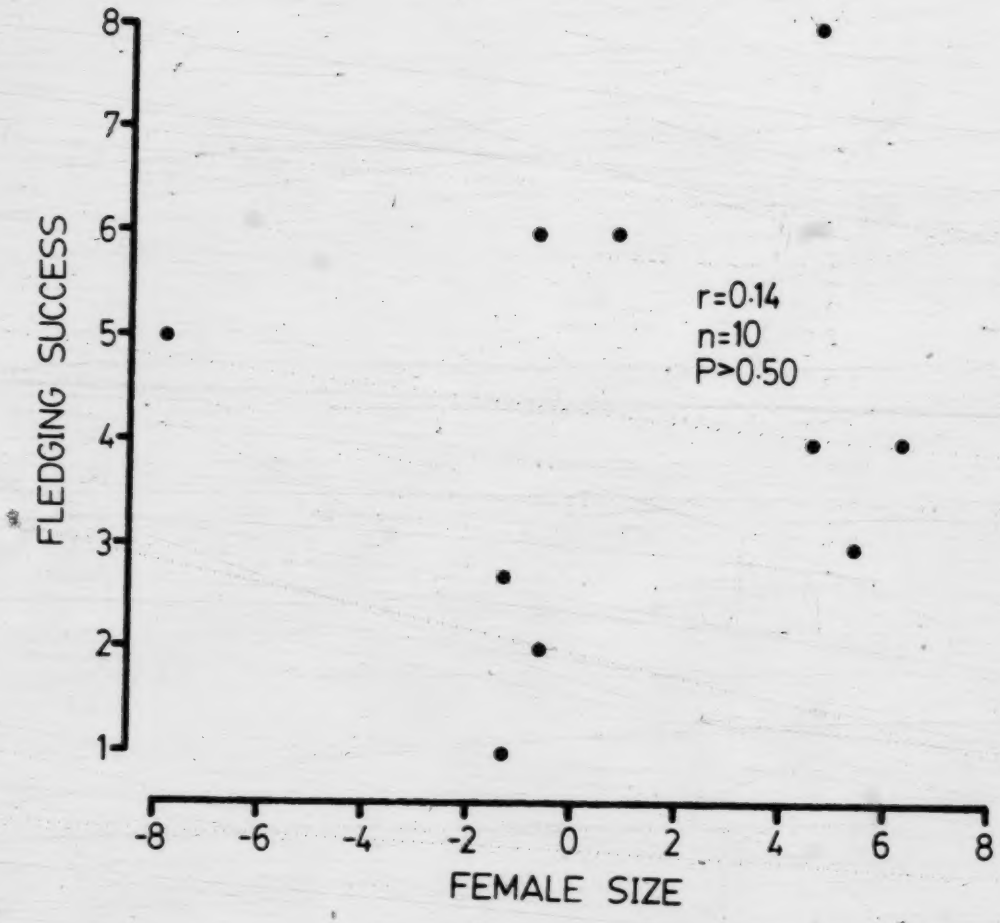
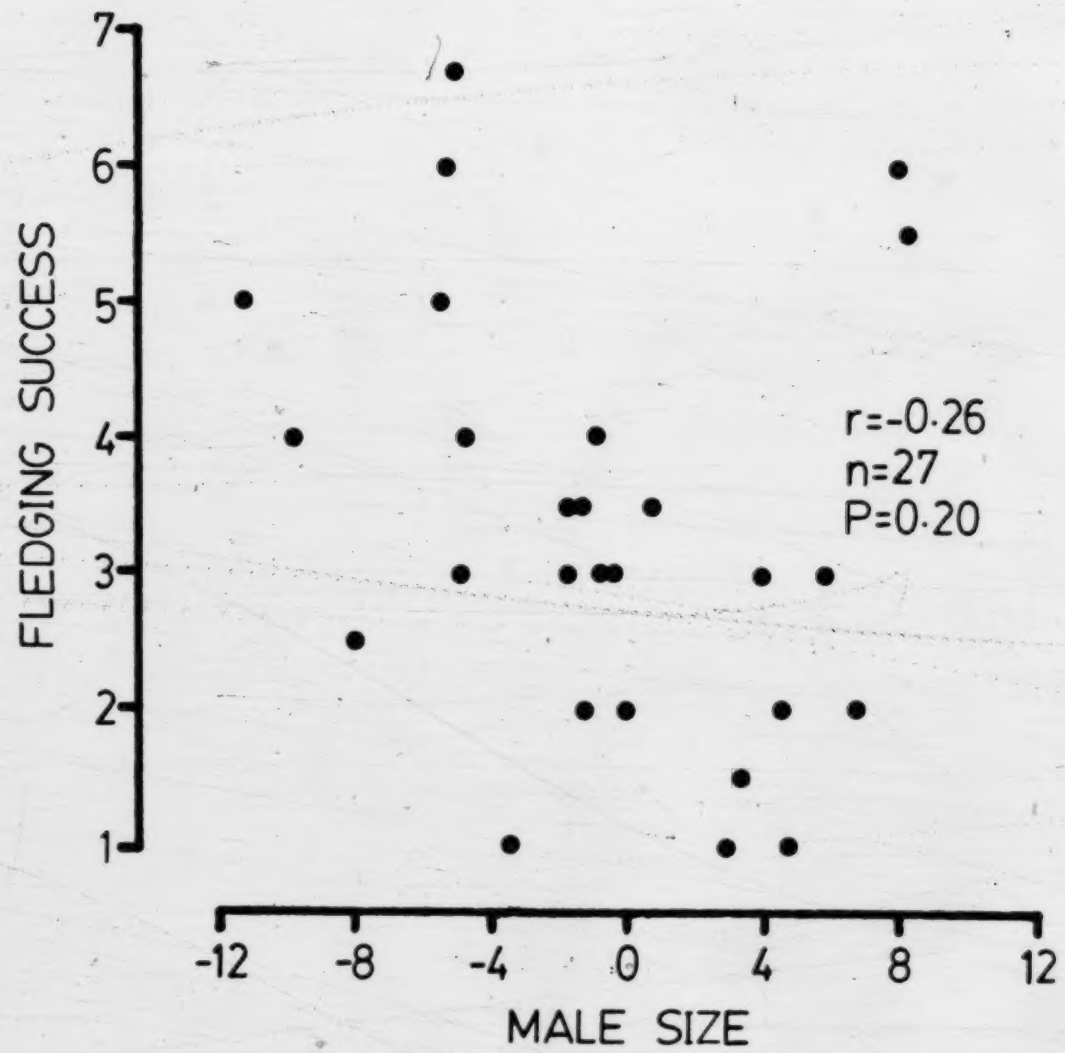


Figure II-9: Relationship between fledging success (averaged, if more than one datum was available for a given male) and male size. Size was measured as the sum of standardized measures of body dimensions (see text for explaination of calculation of body size).



fledglings were ordered by laying date of the clutches from which they hatched. Fledglings from nests falling on the median laying data were divided randomly into the early and late categories. There was no significant difference (G=4.44, *d.f.*=1, *P*=0.50) in the frequency with which early (14 of 46) and late (5 of 46) fledgling remained alive and on the study area into at least their first spring.

Summary

Fledging success decreased through the breeding season, although clutch size showed only a trend in the same direction. There was a weak indication that female size was positively related to clutch size. Clutch size was weakly and non-significantly correlated with the number of fledglings produced from a nest. Territories produce similar numbers of fledglings in consecutive years. After fledging, neither birds from earlier nests, nor those that were heaviest members of their brood lived longer / dispersed significantly less than other fledglings, although there was a trend for heavier siblings to be found longer on the study area.

DISCUSSION

Inter-habitat Variation in Reproduction

Differences were found in some of the reproductive parameters measured among years, habitats, and territories. Laying date was the only parameter to vary significantly among years (Table II-1). This variation was with respect to calender date. Photoperiod, which controls gonadal growth (*e.g.* Murton and Westwood 1977) sets limits to the laying period. But within the limits imposed by photoperiod, environmental temperature (Storey and Nicholls 1982, Wingfield *et al*. 1983) and food availability (*e.g.* Kallander 1974, and Chapter III of this thesis) can influence date of clutch initiation. Precipitation (O'Connor 1979) and the number of degree days in the months preceding laying (Lack 1966, p. 19) have also been shown to be correlated with laying date; the latter two environmental factors may influence laying date through their effects on food availability. Differences in mean laying date among years could reflect different dates on which environmental cues triggered laying, or annual differences in the availability of resources such as invertebrate

prey species. If annual differences in resource availability did exist, they should have been manifested not only in laying date, but also in clutch size or fledging success. Since this was not the case (Tables II-2, II-5), annual variation in laying date probably reflected a variation in the timing of the environmental cues that triggered laying.

Some of the reproductive parameters also varied among the three habitats. Thus, the arbitrarily defined habitat types appear to have some impact on the reproductive success of magpies, and that the birds did not restrict themselves to only the highest quality areas. Whether differences among areas influence nesting density, or saturation of the habitat (*sensu* Krebs 1971) is not known.

The factor(s) triggering the onset of laying appeared to be synchronized among habitats. Mean laying date did not differ significantly among habitats in 3 of 4 years. Annual changes in laying date tended to be synchronized among habitats; earlier laying in one habitat coincided with earlier laying in the other two habitats. Clutch initiation was not consistently earlier in one habitat than any other. This indicates that the differences in egg size and fledging success among habitats are generally not related to differences in laying date (and thus to differences in the time that resources reached the required thresholds to trigger the onset of laying).

Habitat specific differences in clutch size have been noted for great (*Parus major*) and blue tits (*P. caeruleus*) (Lack 1966, p. 25; Perrins 1979, pp. 205-208) and house sparrows (*Passer domesticus*) (Lowther 1979), this difference being explained as a response to a difference in the quality of resources in the habitats (Klomp 1970). However, magpie clutch sizes did not vary significantly among habitats (0.5 eggs or less per nest) (Table II-2). If birds regulate their clutch sizes as the mechanism to control their annual reproductive output (Lack 1966, Crossner 1977), one would expect equal numbers of fledglings from nests on the three habitats (as equal clutch sizes were present). This was not the case; however, farm habitat nests, which had the highest fledging success, also tended to have larger clutches (Table II-4). Thus factor(s) other than clutch size influence the reproductive success of magpies in Edmonton.

Parsons (1970) and Thomas (1980) showed for two gull species that egg size variation among nests was correlated with chick survival, with chicks from larger eggs having higher survival rates. There was a trend for magpie eggs to differ in size among

habitats, with the largest eggs on the farm habitat. One would predict that more fledglings might be produced from farm habitat nests on the basis of egg size; although this was the case, the causality of this relationship has not been established. Egg size and composition are discussed more thoroughly in Chapter IV.

The principal reason for making comparisons among habitats was to provide background information necessary for the analyses carried out in Chapter III. The inter-habitat comparisons also suggest patterns in the way magpie reproduction varied among territories of presumed different quality: high quality habitats having better fledging success, but with slight if any increase in clutch or egg size and no difference in laying date. It was not possible to access the degree of difference among habitats, as the environmental parameters on which to base such measurements are unknown. Thus, although clutch size was not found to differ among habitats, differences in clutch size might be found if other (more extreme) habitats were examined.

Territory and Parental Quality

A partial correlation analysis among nests showed that fledging success declined through the breeding season. However, the correlation was very weak, accounting for only 5.4% of the variance in fledging success. In Edmonton, magpie clutch size tended to decline throughout the breeding season. Tatner (1982) observed a weak, significant (r^2=0.05) decline in magpie clutch sizes over the breeding season in a magpie population in Manchester, England, but he did not find a significant seasonal decline in fledging success. Seasonal decline in clutch size has been noted for a number of bird species (Klomp 1970). It has been suggested that late laying and smaller clutches are generally layed by birds which occupy poor quality territories (Klomp 1970, Newton and Marquis 1984), irrespective of any seasonal decline in food availability (*e.g.* Perrins 1979, p. 201).

For clutches on poor territories to be consistently later and smaller, clutch size must be under environmental control to some extent. Potentially, poor quality birds could consistently have occupied some territories, but even this phemonenon would indicate that there was some characterictic of the "poor" territories which resulted in poor quality birds settling there (annual turnover of breeding birds on territories being high). Territory quality affected clutch size in a Swedish magpie population (Högstedt 1980) in which over 80% of

the variation in clutch size could be accounted for by inter-territory differences. A positive correlation of clutch sizes between years on a territory would be expected, if territory quality played an important role in determining clutch size (either directly, or through physiologically similar birds settling on territories each year). No such correlation was found in Edmonton (Figure II-4). Thus, there was no indication that clutch size was affected by territory quality, and hence that later, smaller clutches were a consequence of poor quality territories in Edmonton.

The sharp contrast between the levels of territorial influence on clutch size in Edmonton and southern Sweden could be due to differences in either the habitat or the magpies. The habitats could differ in two ways. First, the analyses conducted by Högstedt (1980) and I use the degree of predictability of reproductive success on a territory between years, as the measure of the importance of territory quality in reproduction. It was assumed that a high quality territory in one year would remain a high quality territory the next year. Potentially, this assumption could be valid in Sweden, yet not in Edmonton. This seems unlikely, however, as a positive correlation was found for fledging success on a territory between years (Figure II-5); this correlation implies that territory quality is consistent between years in Edmonton. A second possible difference between habitats could be that whatever environmental factor(s) influence magpie clutch sizes in Sweden do not vary sufficiently in Edmonton to affect clutch size. Differences in the degree of genetic (or other intrinsic) control of clutch size could also produce the differences between Edmonton and Sweden. Inter-population differences in genetic control of some characteristics may exist (see James 1983, for evidence of this for some morphological traits of red-winged blackbirds (*Agelaius phoenicus*)). If this were true for magpie clutch size, a higher heritability in Edmonton, coupled with high annual turnover of females on a territory (82% annual turnover estimated) would mean that little if any correlation would be expected among clutch sizes on a territory in consecutive years. Whatever the reason, environmental differences were not found to have an effect on magpie clutch sizes in Edmonton.

Unfortunately, insufficient data were available to determine the degree to which magpie clutch size was regulated by intrinsic factors. There was a weak trend for larger female magpies to lay larger clutches (Figure II-6), even with the small sample (n=13)

available. Larger bodied females may be able to store more nutrient reserves and thus produce larger clutches; the converse, that smaller females produce larger clutches, has also been suggested (Jones 1970). A very small number of females (n=6) produced clutches of known size in consecutive years; there was no apparent relationship between a female's clutch sizes in one year and the next (r=0.04). Thus, evidence (Figure II-6) that clutch size is under some intrinsic control for Edmonton's magpies is very weak.

Clutch size, in fact seems relatively unimportant in determining the reproductive success of magpies in Edmonton. Clutch size was only weakly correlated with fledging success (r^2=0.03, P=0.07). This was also seen in Manchester, England where, although significant, the coefficient of determination between clutch size and fledging success was also very small (r^2=0.11) (Tatner 1982). In Manchester, a better correlate of fledging success was the number of young alive shortly after hatching; apparently, differential mortality occurs near or before hatching (Tatner 1982). Whether the mortality was through differences in hatchability, or brood reduction shortly after hatch was not known. Högstedt (*pers. comm.*) found nestling mortality to occur mainly at two stages: within about 2 days of the nestlings hatching, and near the time that the young fledged. Whatever the reason, variation in clutch size appeared to be of little adaptive significance for Edmonton's magpies.

Fledging success was similar on a given territory in consecutive years (Figure II-5). This effect could be explained as either territorial quality or parental quality (the same breeding birds occupying the same territory in consecutive years) influencing fledgling production. However, as annual turnovers of males and females on a territory were high, 65% and 82% respectively, it is unlikely that the correlation in Figure II-4 was due to parental quality. I therefore conclude that territory quality is important in determining fledging success. Whether the territory directly (*i.e.* through food availability) affected reproduction, or influenced the quality of the birds which settled on it is not known. There is also slight indication that parental quality could affect fledging success: males which shifted territories tended to produce similar numbers of fledglings on these territories (r=0.73, 0.05<P<0.10, n=6). That inter-male differences may play a role in reproductive success was also suggested by Reese and Kadlec (1985), who found that male magpies with breeding experience had a lower percentage of nest failure, regardless of their

mates breeding experience. The only other factor that I examined with regard to fledging success was egg size, and no relationship was found (Figure II-3). Thus, territory quality appeared to affect fledging success, and there was slight indication that inter-male differences also played a role, but data were insufficient to determine the relative importance of intrinsic and extrinsic factors.

Interestingly, male size did not influence reproduction. This suggests that male dominance, as indicated by male size (Scharf 1985), had no effect on reproduction. Dominant males might be expected to acquire better quality territories (Smith 1976, Reese and Kadlec 1984). This probably did not occur because magpie territories are not acquired each year, but are retained throughout the year (Baeyens 1981b). Territories would become open at irregular intervals, and even if the most dominant non-territorial bird were to acquire the open territory (Charles 1972, Baeyens 1982b), there is no guarantee that this territory would be the best available. With such a system no relationship would be expected between a bird's dominance status and the quality of its territory. Of course body size, if heritable, could affect post-fledging survival of young through their dominance status (Scharf 1985).

Variation in post-fledging survival will also affect the reproductive success of breeding magpies. Disadvantages of late laying and fledging have been noted for snow geese (*Chen caerulescens*) (Cooke *et al*. 1984) and great tits (Perrins 1979, p. 202). For Edmonton's magpies no significant difference in overwinter survival / dispersal was noted between fledglings from early and late nests. However, because of the low rates of return of fledgling magpies, sample sizes in the analyses were small. Fledging weight has been linked with survival in great tits (Perrins 1965), the differences being between and not within broods (Lack *et al*. 1957). Because of the methods used, I was only able to look for weight-survival relationships within magpie broods. Weight appeared to affect survival / dispersal, heavier siblings tending to be found longer on the study area. This effect could be sex-related, as there is a tendency in magpies nearing fledging for males to be heavier than females (Scharf, unpubl.). The problem deserves further study.

CONCLUSIONS

In evolutionary terms, the only factor relevant to the fitness of breeding birds is the number of progeny which enter the breeding population. The closest accurately measured parameter in this study was the number of fledglings produced per nest. Fledging success was found to vary through the breeding season, with some territories consistently producing more fledglings than others. The observed variation in clutch size had little effect on fledging success.

There has been much consideration of the significance of clutch size (*e.g.* Lack 1966), including experimental manipulation of brood sizes (Crossner 1977, Schifferli 1978, Högstedt 1980, Loman 1980) from which conclusions have been drawn concerning the optimality of natural clutch sizes. It has been suggested that different clutch sizes are optimal for the territories on which they were produced (Loman 1977, 1980, Schifferli 1978, Högstedt 1980), and that the optimum will be reflected in a constant ratio of fledglings:eggs in nests (Alerstam and Högstedt 1983). Implicit in all of this is the assumption that clutch size is an important correlate of fledgling production. This was not the case for urban populations of magpies in Edmonton or Manchester (Tatner 1982). These data show that the observed natural variation in clutch size may be neither adaptive nor maladaptive in nature, but neutral in its consequences for some species of birds.

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Chapter III

THE EFFECT OF SUPPLEMENTAL FEEDING ON THE REPRODUCTIVE OUTPUT OF BLACK-BILLED MAGPIES IN EDMONTON, ALBERTA

INTRODUCTION

Magpies occupying different territories produce different numbers of eggs and fledglings. Data presented in Chapter II suggest that some of the variation, at least in fledging success, is due to differences among territories (an environmental effect), rather than among birds (a biological effect). Environmental factors suggested to influence reproduction include predation pressure (*e.g.* Yom-Tov 1974), suitability of nest sites (*e.g.* Balda and Bateman 1972, O'Connor 1978, McGillivray 1981), weather during the breeding season (*e.g.* Murphy 1983), and the availability of food (*e.g.* Newton 1980). In order to test the last factor on reproductive output, one must systematically manipulate the food supply of breeding birds (Newton 1980). One such manipulation was a study in Sweden in which supplemental food was provided to breeding magpies (Högstedt 1981). In that study, food supplementation advanced laying and increased clutch size, egg size, and fledging success. However, it was not shown whether the advanced laying and increased clutch and egg size produced the higher fledging success, or whether higher fledging success was the independent result of food shortage during nestling rearing. This chapter describes food supplementation experiments the results of which can be contrasted to those of Högstedt (1981) and food supplementation studies of others, as well as attempting to determine the time(s) during the breeding cycle when the natural food supply is most limiting.

METHODS AND RATIONALE

Food supplementation was carried out during the breeding seasons of 1982-84. It is important that a supplemental food be of sufficiently high nutritional quality that it will act as a true supplement, both qualitatively and quantitatively. The supplemental food used was Wayne brand, dry, pelleted dog food. Its composition, in comparison to an optimal diet for some galliforms and anseriforms, is given in Table III-1. The supplemental food was judged suitable because it was successfully used in maintaining captive magpies, one pair of which produced a viable clutch in captivity. The dog food was also used to hand-rear nestling magpies from an age of roughly 10 days to independence (P. Fraser, *unpubl.*). A more detailed consideration of the nutritional suitability of the dog food is given in the discussion of this chapter.

Table III-1: Estimated nutritional requirements for pheasant, northern bobwhite (*Colinus virginianus*), ducks, geese, and wild turkey (*Meleagris gallopavo*) producing eggs ("breeding") and for growth of young ("growing") (Scott 1972), compared with the composition of the supplemental dog food provided to magpies.

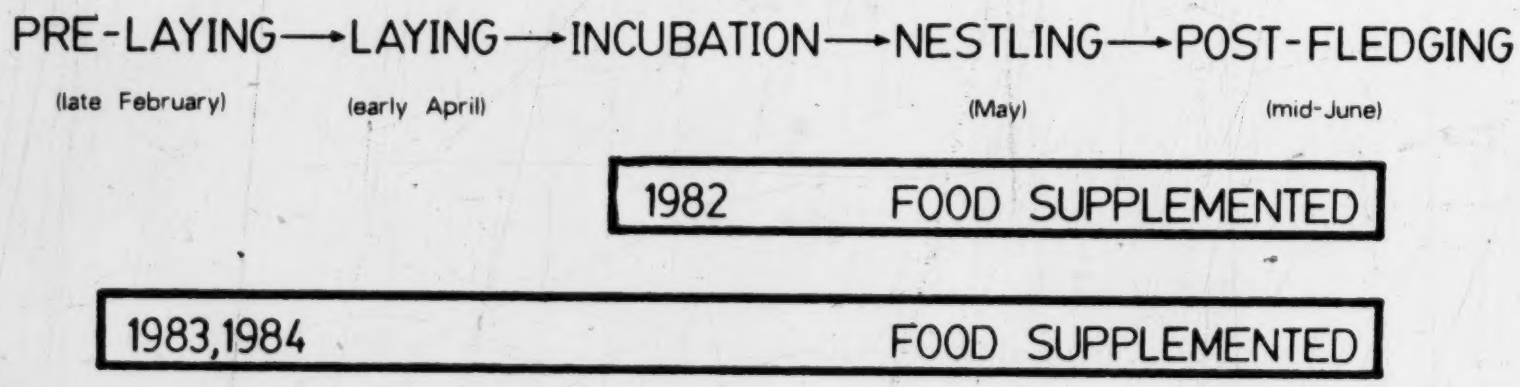
Constituents	Diet		
	Breeding	Growing	Supplement
Protein (%)	19	24	25
Calcium (%)	2.7	0.7	2.1
Phosphorus (%)	0.5	0.45	1.4
Sodium (%)	0.1	0.1	?
Chloride (%)	0.15	0.15	?
Potassium (%)	0.6	0.6	0.55
Manganese (ppm)	70	70	80
Zinc (ppm)	60	60	140
Magnesium (ppm)	350	400	1800
Iron (ppm)	130	90	220
Copper (ppm)	13	9	13
Iodide (ppm)	0.3	0.3	1.4
Selenium (ppm)	0.1	0.1	0.1
Vit. A (IU/kg)	13000	10000	11500
Vit. D_3 (IU/kg)	1500	1500	?
Vit. E (IU/kg)	25	10	50
Vit. K (IU/kg)	0.5	0.5	?
Riboflavin (mg/kg)	3.5	3.5	4.1
Nicotinic acid (mg/kg)	60	60	42.8
Pantothenic acid (mg/kg)	15	8	11.5
Vit. B_{12} (mg/g)	500	300	2000
Choline (mg/kg)	1100	1500	1300
Linoleic acid (%)	1.5	0.8	2

The rationale for using the dog food was that it would serve as a supplement to the food already on a territory. The purpose was not to have breeding magpies feed exclusively on the dog food, but for them to use the supplement only to the extent that it would make up for short-falls in the natural food supply (raise the quality of the territory's food resources). It was assumed that a combination of natural and supplemental food met all nutritional requirements of breeding magpies, and that magpies would forage selectively for required nutrients (*sensu* Fogden and Fogden 1979, Krapu 1981).

On each food supplemented territory, a feeder was attached to a tree, usually within 5 m of the base of the nest tree. Each feeder was capable of holding slightly over 1 kg of dog food. In 1982 the dog food was provided *ad libitum*, but in 1983 and 1984 the maximum rate of use was set at 1 kg/fortnight. This limit was set because territorial magpies cached large amounts of the supplemental food during the early parts of the breeding cycle. Logistics did not permit the distribution of an *ad libitum* supply of food. A limit of 1 kg/pair/fortnight was considered reasonable because, in captivity, magpies required 15 g of dog food/bird/day for maintenance in winter (Scharf, *unpubl.*). The 1 kg of dog food provided, exceeded the 420 g required by a pair of magpies, even if they were to rely solely on the dog food.

If the availability of natural food limits breeding success, food limitation may not occur throughout the breeding cycle, but for only short parts of the cycle, creating a "bottleneck". To investigate this possibility, provisioning was begun at two different times in different years (Figure III-1). In 1982 feeding was begun after the eggs were laid; if fledging success of birds on territories on which supplemental feeding occurred (the experimental group) was greater than that of birds on non-supplemented territories, it would imply a food shortage at some time between the latter part of incubation and the time the young fledged. In 1983 and 1984 supplemental feeding began roughly 1 month before eggs were laid. Supplemental feeding throughout the breeding cycle might influence date of clutch initiation, clutch size, egg characteristics, or fledging success. The supplementation in 1983-84 was not stopped at incubation (in order to give a distinct pre-hatching supplementation effect) for two reasons. First, since magpies cache food on their territories, a stop to supplemental feeding would not mean that territories returned to natural levels of food availability. Second, there is the possibility of a synergistic effect;

Figure III-1: Stages of the breeding cycle of black-billed magpies at which supplemental food was available on experimental territories.



pre-laying provisioning with supplemental food could result in the birds laying a larger clutch "in expectation of" a high quality territory later in the breeding season. If withdrawal of the supplemental food lowered territory quality during the latter part of the breeding cycle, breeding success could be even lower than on control territories (see Reese and Kadlec (1984) for an apparently similar effect of withdrawal of supplemental food between the time of territory establishment and the onset of laying).

Supplemental feeding was done in some territories on all three habitats (urban, farm, and river valley; Figure II-1) in 1982 and 1983. In 1984 only urban and river valley habitats were used. However, in 1984 few nests (n=6) in the urban habitat were supplemented; from all nests on the river valley habitat (supplemented and non-supplemented) entire clutches were removed for analysis of egg composition (Chapter IV). Thus, for 1984 few data were available for comparing fledging success on supplemented and control territories. In 1982 the territories to be supplemented were chosen at random; for this reason, supplemented and control territories tended to be interspersed. In 1983 and 1984 supplemented and control areas were set out in blocks of 5-10 territories; supplemented and control territories were not interspersed. The latter procedure was followed to insure a representative collection of nests in each block. Feeders were not placed on territories until after nest construction was observed. As nest construction did not begin simultaneously on all territories, some means was required to insure that nests started at various times were included in both food supplemented and control groups. Feeding in all territories in certain blocks fulfilled this purpose. In practice, this procedure meant that feeding was begun on territories over a 2 week period.

The parameters measured were laying date, clutch size, number of nestlings banded at or after 14 days of age (taken to be the number of young fledged). Data are presented as $\bar{x}\pm$s.d. (n). All statistical analyses were done on BMDP (Dixon *et al*. 1983) computer programs unless otherwise noted.

RESULTS

Food Use

Supplemental food disappeared from feeders throughout the breeding cycle (Figure III-2) and it is assumed that magpies were largely responsible (but see discussion). The rate of food disappearance was not uniform throughout the season, being highest before egg laying began; the variability of use among territories increased after this point in the breeding cycle.

Reproductive Parameters

Laying Date

Laying dates recorded in 1983 and 1984 are summarized in Table III-2. These were the 2 years that supplemental food could have affected the onset of laying since it was added to territories before egg laying. In 1983, clutch initiation was earlier on supplemented territories. For 1984, when clutch initiation was significantly later in urban than river valley habitat (control territories) (Table II-1), separate comparisons were made for these two habitats. Only in the urban habitat was clutch initiation earlier on food supplemented territories.

Clutch Size

As clutch size on control territories did not differ among habitats (Table II-2), data were combined. Differences in clutch size did not exist between 1983 and 1984, either for control (Table II-2), or experimental territories (1983—6.76±1.25 (17); 1984—7.00±0.01 (13); t=0.65, P=0.52 t-test on samples of unequal variances). Data were also combined for the two years for each treatment group. Clutch sizes were slightly higher on territories with supplemental food (control 6.47±1.07 (55); supplemented 6.87±1.04 (30); t=1.64, P=0.11). The effect, however, was not strong.

Fledging Success

The rate at which nesting attempts completely failed was not reduced with supplemental feeding, regardless of whether supplemental feeding began before or after

Figure III-2: Rate ($\bar{x} \pm 1$ S.E.) of disappearance of supplemental food from feeders at different stages during the black-billed magpie reproductive cycle.

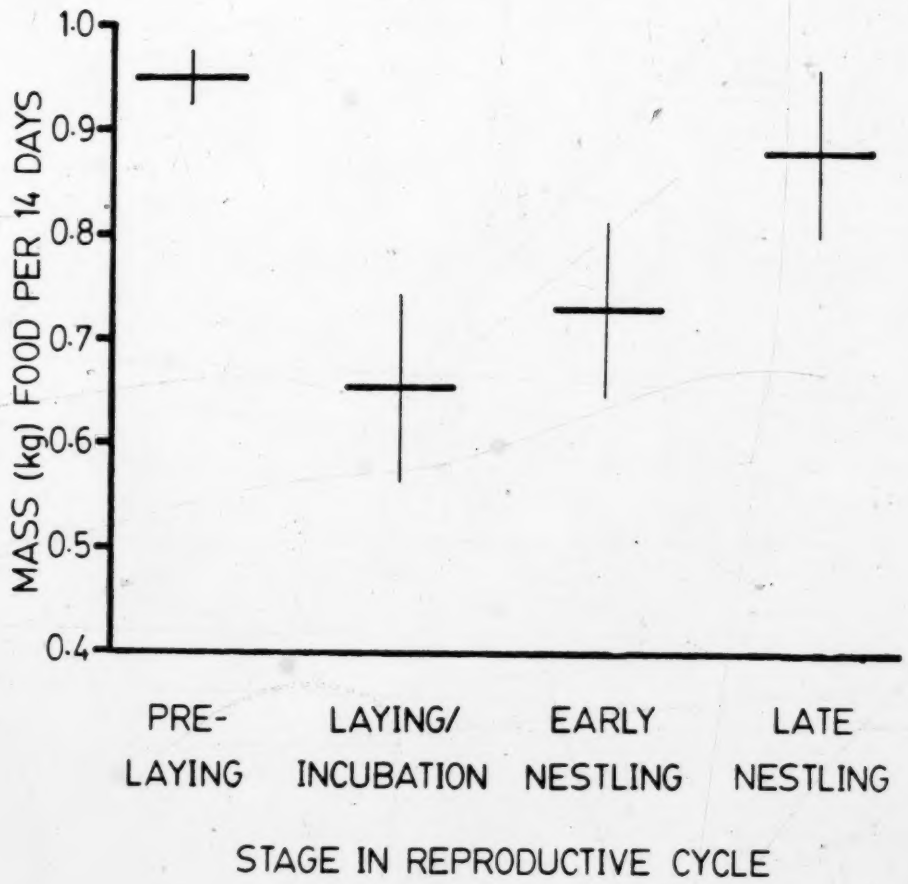


Table III-2: Date of clutch initiation [$\bar{x}$±s.d. (n)] for magpies occupying control territories, and territories on which supplemental food was provided.

Year (Habitat)	Treatment		Probability
1983 (Urban and River Valley)	Supplemented	Apr. 17±4.6 (16)	P=0.007
	Control	Apr. 23±5.2 (11)	
1984 (Urban)	Supplemented	Apr. 11±7.2 (5)	P=0.01
	Control	Apr. 19±5.0 (15)	
1984 (River Valley)	Supplemented	Apr. 6±6.0 (6)	P=0.81
	Control	Apr. 6±6.0 (6)	

clutch initiation (Table III-3). In fact, in 1984 the nests on food supplemented territories failed significantly more often than those on control territories.

For those nests which produced at least 1 young, fledging success was not affected when supplemental feeding was begun after laying (Table III-4). In 1983, when feeding began before laying, fledging success was significantly better on food supplemented territories (Table III-5). In 1984, even with very small samples in only the urban habitat, there was a tendency for higher fledging success with supplemental feeding (control 3.80±1.67 (20); supplemented 4.67±0.58 (3); t=1.73, P=0.12, t-test on samples with unequal variances).

Re-laying

An effect of supplementation was noted in 1984, on territories where clutches of eggs had been removed. The frequency of renesting after egg removal was higher on supplemented (5 of 8) than control (3 of 13) territories (G=3.03, $d.f.$=1, P=0.08).

DISCUSSION

Methodology

Food supplementation experiments have been carried out during the breeding season on a number of passerine species: carrion crow (*Corvus corone*) (Yom-Tov 1974), magpies (*Pica pica pica*) (Högstedt 1981), willow (*Parus montanus*) and crested tits (*P. cristatus*) (von Brömssen and Jasson 1980), great tits (*Parus major*) (Jones 1973, Källander 1974), red-winged blackbirds (*Agelaius phoeniceus*) (Ewald and Rohwer 1982), and song sparrow (*Melospiza melodia*) (Smith *et al*. 1980). One basic problem in food supplementation experiments is providing a food that is nutritionally suitable for the breeding birds under study. For example, Jones (1973) felt that the sunflower seeds used in his experiments may have been deficient in an essential amino acid, lysine.

The dog food used in this study appeared to be nutritionally suitable for the breeding magpies. Unfortunately, I could find no references on the nutritional requirements of breeding altricial birds. However, a comparison of the dog food composition to the nutritional requirements of a number of precocial species (Table III-1)

Table III-3: Number of nesting attempts that successfully fledged at least one nestling, or failed to produce any young. Comparisons are between control and food supplemented territories within each year.

	1982		1983		1984	
Treatment	Fledged	Failed	Fledged	Failed	Fledged	Failed
Supplemented	20	8	16	5	3	3
Control	29	17	21	6	20	2
Probability[1]	$P>0.50$		$P>0.50$		$P=0.05$	

[1]Probabilities determined by G-tests, with William's correction factor.

Table III-4: Fledging success [$\bar{x}$±s.d. (n)] of black-billed magpies in 1982[1]. . Feeding was started on "supplemented" territories after laying. Only data from nests from which at least one nestling fledged were used.

	Habitat		
Treatment	Urban	Farm	River Valley
Supplemented	2.4±0.9 (5)	5.2±0.8 (5)	3.8±1.6 (10)
Control	3.7±1.9 (18)	5.2±1.9 (6)	2.8±1.3 (5)

[1]For a two-way ANOVA among treatments and habitats: treatment P=0.88, habitat P=0.004, treatment X habitat P=0.19.

Table III-5: Fledging success [$\bar{x}$±s.d. (n)] of black-billed magpies in 1983[1]. Feeding on "supplemented" territories was begun before clutch initiation. Only data from nests producing at least one fledgling were used.

	Habitat		
Treatment	Urban	Farm	River Valley
Supplemented	5.4±2.4 (7)	5.7±1.5 (3)	3.7±1.5 (6)
Control	2.8±1.4 (13)	4.0±2.0 (3)	2.6±1.8 (5)

[1]For a two-way ANOVA among treatments and habitats: treatment P=0.01, habitat P=0.16, treatment X habitat P=0.49.

showed that the dog food met or exceeded most nutrient requirements of laying females and growing chicks. Thus, compositionally the dog food appeared suitable. As well, as already noted, captive magpies were capable of growing, producing viable eggs, and being maintained when this food was their staple diet.

A second methodological problem encountered in food supplementation experiments is whether the food that disappears is actually used by the experimental subjects. Yom-Tov (1974) gave evidence that the supplemental food he provided was taken to the nests and eaten by chicks of carrion crows. Other studies merely noted the disappearance of the supplemental food. I observed magpies taking the dog food, but I have no evidence of them feeding it directly to nestlings. The supplemental food was taken throughout the breeding cycle (Figure III-2), the highest and most consistent use being during the pre-laying period. Subsequently the rate of disappearance and assumed use decreased. If the rate of disappearance of supplemental food is inversely proportional to the abundance of natural food, the data in Figure III-2 suggest that the time at which natural food was least abundant was the pre-laying period. However, "use" could indicate both actual ingestion and caching of supplemental food. Thus, the rate of disappearance of supplemental food gave no clear indication of the degree of shortage of natural food for magpies, although subjectively food seemed least available during pre-laying.

A third methodological problem is that animals other than those intended may take some of the supplemental food. No marked magpies were observed taking food from a feeder on other than their own territory. Other species, however, took food from feeders. In two instances starlings (*Sturnus vulgaris*) were seen at feeders. Also, over the 3 years of supplemental feeding I found evidence of red squirrels (*Tamiasciurus hudsonicus*) taking food from roughly 10 of the 28 feeders placed out in the river valley habitat. I do not know how much food was taken by other species. Use of feeders, particularly by squirrels, undoubtedly reduced the amount of supplemental food available on some territories. Nevertheless, even if half the food was removed by other species, the total minimal food requirements of the adult magpies could still be met by the supplemental food. Because of food removal by other species, and the caching of food by magpies, I have not used the data on food disappearance rates beyond simply noting the changing rate over the breeding season (Figure III-1).

The problems noted above are common to all food supplementation studies. Each of the problems has been discussed, to the extent possible, with respect to the present study. The degree to which these problems, particularly the use of food by other species, affected this study is not known. However, where differences were found between supplemented and control territories, the most parsimonious explanation is that the presence of supplemental food, regardless of the amount consumed by the magpies, produced the observed results.

Reproductive Parameters

Clutch Initiation

The results recorded in this study are consistent with some previous food supplementation studies on passerines in showing laying advanced by a few days on food supplemented territories (Table III-2). The exceptions were Jones (1973) who did not advance clutch initiation of great tits, and Smith *et al*. 1980 and Ewald and Rohwer (1982) who found an advancement of 2 weeks or more. Collectively, food supplementation experiments indicate that the onset of laying can be influenced by the availability of food. However, at a proximal level, birds do not begin laying as soon as sufficient food is available, or one would expect laying to be advanced almost to the time at which the supplemental food became available, assuming a completed nest was available. Food availability appears to affect clutch initiation only within the narrow limits established by other factors such as photoperiod (*e.g.* Murton and Westwood 1977), and temperature (*e.g.* Storey and Nicholls 1982).

Food availability may not be the factor limiting laying date in all cases. In 1984, the addition of supplemental food advanced magpie clutch initiation only in the urban habitat (Table III-2); laying was also significantly later in the urban than farm or river valley habitats in 1984 (Table II-1). It appears that natural food levels were lower in the urban habitat early in the 1984 breeding season, resulting in both later laying and a response of clutch initiation date to supplemental feeding in that habitat.

Clutch Size

In the city of Edmonton, clutch size of magpies was not significantly affected by food supplementation, although the probability level of the test (P=0.11) weakly suggested an increase in clutch size with supplementation. In Sweden, supplemental feeding of magpies produced a significant increase in clutch size in only 1 of 2 years (a mean increase of 0.6 eggs / nest); in the second year the increase only approached statistical significance (Högstedt 1981). The results from Edmonton are consistent with Högstedt's (1981) findings of increased clutch size with supplemental feeding. However, even if the clutch size increase found in Edmonton was real, the small magnitude of the change probably made any increase in parental fitness negligible because the correlation between clutch size and fledging success is small (r^2=0.03, Chapter II).

The evidence for limitation of clutch size by nutrient availability is conflicting. Most food supplementation studies (Yom-Tov 1974, von Brömssen and Jasson 1980, Smith *et al*. 1980, Ewald and Rohwer 1982) did not show any effect of increased food availability on clutch size. In fact, Ewald and Rohwer (1982) noted a decrease in clutch size with supplemental feeding; they attributed this decrease to a correlation (only seen for the earliest clutches in the year, and typical of some species (Klomp 1970)) between earlier laying (an effect they found with supplementation) and smaller clutch size at the start of the breeding season. The studies cited above suggest that food availability does not limit the sizes of clutches produced by some species.

However, studies on other species indicate that food availability can affect clutch size. In years of low natural food levels, food supplementation increased clutch size of European kestrels (*Falco tinnunculus*) (Dijkstra *et al*. 1982), and nutcrackers (*Nucifraga caryocatactes*) (Swanberg, data presented in Lack 1954, p. 30). Jones and Ward (1976) showed that the nutrient stores in female red-billed quelea (*Quelea quelea*) (and presumably the availability of food to these birds) could influence clutch size. For other species less direct evidence was found. In dry years (with poor food supplies?) some Australian species laid smaller clutches, if they bred at all (Serventy 1971). Swanberg (in Lack 1954) showed that nutcrackers laid larger clutches in years with unusually good hazelnut (*Corylus avellana*) crops. Newton (1979, pp. 131-134) provides a review of falconiform species whose clutch sizes vary directly with the abundance of their cyclic prey. Klomp (1970)

notes that clutch sizes of various owls and white stork (*Ciconia ciconia*) are correlated with prey availability; prey types were not given, but presumably are cyclic rodent species (*e.g.* Southern 1957, for tawny owl (*Strix aluco*); Lack 1966, p. 214 notes that white storks prey on cycling *Microtus arvalis*). Bay-breasted warblers (*Dendroica castanea*) have been noted to produce slightly larger clutches when spruce budworm outbreaks occur (MacArthur 1958).

With the exception of the magpie (Högstedt 1981), all of the species noted in the previous two paragraphs, for which natural food supply appears to limit clutch size, depend upon a highly fluctuating food supply. The raptors and stork fed on cycling microtines. The Australian species and quelea live in arid regions where rainfall (and food supply) are unpredictable and variable; this unpredictability is so great that quelea may even be forced to abandon nesting colonies because of lack of food (Jones and Ward 1979). The hazelnut crops upon which the nutcrackers feed are irregular in abundance (Lack 1954). The spruce budworms on which bay-breasted warblers feed can vary greatly in numbers. If food abundance varies widely it would not be surprising that in some years food availability would be low enough to limit the clutch size of birds. I suggest that all species may at times have clutch size restricted by food availability; however, for the species in which this phenomenon has been noted, the frequency of occurence may be greater than for other species for which food quality and quantity are seldom a problem.

Fledging Success

In 1982, when food supplementation started after clutches were complete, fledging success was not affected (Table III-4). Apparently food was not limiting during the nestling period in that year. In 1983, however, supplemental feeding which was begun before eggs were laid increased fledging success (Table III-5). I conclude that the availability of natural food did limit fledging success of magpies, but that this food limitation occurs during or before incubation.

This conclusion is based on the assumption that the natural food supply was similar during the 1982 and 1983 breeding seasons. This assumption is required because supplemental food was available through the nestling period in both 1982 and 1983 (Figure III-1), and if environmental conditions had varied between the years such that food

was limiting during the nestling period in 1983, but not in 1982, the observed results would also be expected. I have no direct evidence to test this assumption; however, if conditions did differ between these 2 years, one would expect these differences to be manifested in other parameters of magpie reproduction. Clutch size (Table II-2) and fledging success (Table II-4) did not differ between 1982 and 1983 in control nests, and the mean date of clutch initiation only differed by 3 days between these years. The evidence suggests that the only difference between food supplemented nests in 1982 and 1983 was the availability of supplemental food to breeding birds before hatching occurred in 1983.

Given that the natural food supply during the period from clutch initiation to hatching is a limiting factor in magpie reproduction, there are three possible mechanisms by which this limitation could act. First, the availability of the supplemental food near the nest could allow parent magpies to forage close to the nest, and thus better guard against predation (*sensu* Yom-Tov 1974, Spray 1978). Second, as egg production appears to require a large nutrient investment from female birds (*e.g.* Jones and Ward 1976), supplemental food may allow female magpies to be in better nutritional condition after egg laying, thus allowing them to incubate the eggs and rear the nestlings more effectively. Third, with supplemental feeding, magpies may lay better quality eggs, which give rise to better quality nestlings which will be more likely to survive to fledging (*e.g.* Moss *et al.* 1981).

It seems unlikely that supplemental feeding reduced nest predation rates. Predation would likely be manifested by total loss of nest contents (G. Högstedt *pers. comm.*, Yom-Tov 1974), and nests which failed to produce any fledglings were excluded from analyses of fledging success. Högstedt (1981) however, showed that supplemental feeding reduced the rate of nest failure, but did not increase the number of fledglings produced from successful nests in Sweden. If partial predation of nest contents did occur, this predation need not be restricted to the laying and incubation periods (when supplemental feeding appeared to influence magpie reproduction in Edmonton). It should be noted, however, that Ebenman and Karlsson (1984) showed that mortality rates were indeed higher for embryos (eggs) than nestlings of the European blackbird (*Turdus merula*); they attributed this to poorly concealed nests being found early. As magpie nests

are large and (to man) conspicuous structures, the above probably would not apply to magpies.

Thus there seem to be two viable hypotheses concerning the mechanism by which supplemental feeding in the pre-hatching period could influence fledging success: altered egg quality and/or nutritional state of the breeding female. Egg composition data are presented in Chapter IV. It was not possible to determine if nutritional condition of supplementally fed and control females differed during the laying period, because monitoring change in female condition (*e.g.* body weight, fat reserves) would require repeated weighing of the females, which was not feasible. It has been suggested that the initiation of egg laying requires some minimal threshold level of nutrient stores in the female bird (*e.g.* Jones and Ward 1976, 1979); if this is true for the laying of first clutches by magpies, it should also hold for magpies re-laying after their first clutch has been destroyed. Female magpies which re-laid would be expected to be in better nutritional condition than those which did not re-lay. Thus, as supplementally fed female magpies tended to re-lay more frequently than control females in 1984, when their clutches were removed, there is evidence that supplementally fed females were in better nutritional condition after laying their first clutches. Whether better nutritional condition led to more effective parental care is not known.

Conclusions

During the years of this study, it appeared that sufficient natural food was available to produce the sizes of clutches observed; there was only a slight indication (an increase of less than 0.5 eggs per nest with supplemental feeding begun before clutch initiation) that clutch size increased with supplemental feeding. However, the natural supply of food available from pre-laying through incubation influenced clutch initiation and fledging success: the addition of supplemental food resulted in earlier clutch initiation and the production of a larger number of fledglings. Thus, it appears that, in Edmonton, magpie clutch size is less often limited by food availability than date of clutch initiation and/or fledging success.

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Chapter IV

THE COMPOSITION OF BLACK-BILLED MAGPIE EGGS

INTRODUCTION

Of the various characteristics of eggs, their size has been suggested to influence their potential to produce fledglings. In some species, larger eggs are more likely to produce fledglings (Parsons 1970, Schifferli 1973, Howe 1976, Nisbet 1978, Lundberg and Väisänen 1979, Thomas 1980, Moss *et al*. 1981, Järvinen and Väisänen 1984). It may not be egg size *per se*, however, but some factor correlated with egg size that actually affects egg quality (*e.g.* O'Connor 1975). A knowledge of the way in which egg composition varies with size is thus important in understanding the mechanisms by which attributes of eggs can influence the growth and survival of chicks. Additionally, a knowledge of egg composition is needed to assess egg quality because the mass of some egg components may not be correlated with egg size (*e.g.* yolk lipid, Ricklefs 1984a).

In Chapter III it was suggested that the quality of magpie eggs (their likelihood of producing a fledgling) may have been increased with the provision of supplemental food on a territory. By comparing the composition of eggs from food supplemented and control territories it is possible to see whether supplemental feeding influenced egg composition, and whether this effect is consistent with an increase in egg quality. In addition, the data on magpie egg composition may be compared with similar data from other species such as the starling (*Sturnus vulgaris*) (Ricklefs 1984a), and the brown-headed cowbird (*Molothrus ater*) (Ankney and Johnson 1985).

METHODS

Eggs were collected in 1984 and 1985 for analysis of composition. In 1984, entire clutches were collected on either the day on which the last egg of the clutch was laid, or the day after. In only 1 of 21 clutches was there any indication that incubation had begun; in 4 of 6 eggs of that clutch the division between yolk and albumin was noticably breaking down, an event which occurs in herring gull (*Larus argentatus*) eggs within 12 hours of the onset of incubation (Parsons 1976). Complete clutches were collected from 15 nests in the river valley habitat (Figure II-1); 7 clutches came from territories on which supplemental feeding began about 1 month before clutch initiation with an additional single egg coming from an eighth supplemented territory, and 8 clutches came from unmanipulated control territories. A further 5 clutches were removed from nests in the

farm habitat. In 1985 single eggs were collected from each of 18 nests, 10 from food supplemented territories and 8 from control territories,all from the urban habitat.

In the laboratory, egg length and breadth at largest diameter were measured with dial calipers to 0.1 mm. Eggs were weighed, and then separated into wet yolk, wet albumin, and wet shell with membranes. The layer of albumin adhering to the yolk was removed by rolling the yolk on a piece of aluminum foil (Ricklefs 1984). All of the above measurements were obtained within 3 hours of collection of the eggs. Egg components were then dried to constant weight (at 60° C in 1984, and at 40° C in 1985), and then reweighed, water content being determined as the difference between wet and dry mass. Each yolk was then ground up, and neutral lipids extracted with petroleum ether solvent for 2 hours in a soxhlet apparatus. Lipid mass was determined as the residue after evaporating the solvent over a steam bath. All masses were determined to 1 mg on a Mettler balance.

Sample sizes for statistical analyses of egg components varied with the component in question. One clutch of 7 eggs (from a food supplemented territory) apparently had abnormally porous shells, as water loss was noticeable from all eggs, even though they were collected the day after the last egg was laid; data on water content of these eggs were not used. For the clutch in which incubation had begun, it was not possible to separate yolk from albumin in 4 of 6 eggs; thus data on masses of these components were not available for these eggs. Additionally, mishandling caused the breakage of 6 eggs in 1984. In total, 159 eggs, 142 of which had complete data sets, were analysed over 2 years. As well, the lengths and breadths were known for an additional 296 eggs from 45 complete clutches on the urban habitat. These eggs were measured at the nests with the same pair of dial calipers used in the lab. Data were analysed using BMDP programs (Dixon *et al*. 1983) unless otherwise noted.

RESULTS

Egg Size Variation

In this thesis an index of egg volume, the product of egg length and squared breadth at largest diameter (LB^2), will be referred to as egg size. Egg size was more variable among than within nests (Table IV-1). Intra-clutch variance in egg size did not differ between control and food supplemented clutches. Using mean egg size of each clutch as data points, there was no difference in egg size between years (1984 and 1985) or between supplementally fed and control clutches (Table IV-2). Collection of complete clutches in 1984 caused re-laying by some females (Chapter III), and failure of first clutches in 1985 resulted in re-laying by 2 females. Over the two years, mean egg size was known for first and second clutches in 6 cases. Egg size did not change significantly with re-laying (increase in egg size of 0.38±0.76 (6), P=0.28, paired t-test).

Variation in Egg Composition Among Clutches

For each egg component, an analysis of variance was conducted on its mass (Table IV-3); comparisons were between clutches from food supplemented and control territories in the river valley habitat, and farm habitat. Thus it was possible to compare between the composition of control eggs, and eggs from nests with higher productivity, either naturally (farm habitat, Chapter II) or through supplemental feeding (Table III-4). Only yolk lipid mass differed significantly among groups, with differences for lean yolk mass approaching significance. For both yolk components, the greatest difference was between food supplemented territories (small yolks) and farm habitat eggs (large yolks). For only one of five components measured (shell) did the average mass in food supplemented eggs even tend to be higher than that in control eggs. There is no indication that supplemental feeding resulted in the production of eggs with higher nutrient content. As supplemental feeding also did not influence clutch size significantly (Chapter III), the total mass of nutrients in a clutch was not affected by food supplementation.

The mass of each egg component was regressed on egg size in order to determine whether the composition of eggs could be predicted from their size. For eggs collected in 1984, the mean component mass and egg size for each clutch were used as data points;

Table IV-1: Variance in egg size (the product of length and squared breadth at largest diameter) among and within clutches[1], determined by separate one-way ANOVAs on clutches from food supplemented and control territories. Coefficient of determination (CD) is the percentage of variance occurring within clutches.

Source of Variance	Supplemented	Control
Among Clutch	15225.6 (df=11)	16697.9 (df=16)
Within Clutch	738.8 (df=71)	966.4 (df=102)
CD	26.3%	29.8%

[1]F-test comparing within clutch variances showed no significant difference with supplemental feeding ($P>0.10$).

Table IV-2: Variation in the size (the product of length and squared breadth at largest diameter) of black-billed magpie eggs between years, and with and without supplemental feeding[1]. Data are presented as $\bar{x}$±s.d. (n), and the data points were mean egg sizes of clutches.

	Treatment	
	Supplemented	Control
1984	17.4±1.5 (12)	17.1±1.6 (17)
1985	17.3±0.7 (9)	16.7±1.2 (15)

[1]For a two-way ANOVA among years and feeding treatments: treatment—P=0.23, year—P=0.52, treatment X year—P=0.69.

Table IV-3: Mass of components of black-billed magpie eggs [$\bar{x}$±s.d. (n)] from food supplemented and control territories (in the river valley habitat), and from control territories in the farm habitat. Probabilities are from one-way ANOVAs among groups. Data points were mean values for clutches.

	Supplemented	Control	Farm	Probability
Dry Albumin (g)	0.64±0.09 (8)	0.65±0.06 (8)	0.66±0.07 (5)	P=0.95
Lean Yolk (g)	0.28±0.04 (8)	0.30±0.03 (8)	0.32±0.01 (5)	P=0.06
Yolk Lipid (g)	0.33±0.05 (8)	0.36±0.03 (7)	0.39±0.03 (5)	P=0.05
Shell (g)	0.55±0.05 (8)	0.54±0.04 (8)	0.58±0.04 (5)	P=0.32
Water (g)	7.10±0.66 (7)	7.35±0.47 (8)	7.70±0.47 (5)	P=0.19

the data points for 1985 were individual eggs (as only one egg was collected per clutch). Regressions were performed on log transformed data (allometric regressions). Thus a slope of 1 indicates that component mass increased in direct proportion to egg size (a linear relationship). Slopes less than 1 indicate that component mass increased at a lower rate than egg size, and slopes greater than 1 that component mass increased at a higher rate than egg size.

There are two reasons for using the egg volume index, and not egg mass, as the measure of egg size. First, a practical reason is that I consider volume to be more readily measured in the field than egg mass; thus, to predict the composition of eggs on the basis of their size as measured in the field, one must use the same measure in laboratory and field. Second, I am using regression analysis to look for changes in egg composition with respect to egg size; if my measure of egg size varied with egg composition, the purpose of the analysis would be defeated. As egg mass is the sum of component masses, and as egg components have different densities, egg mass will vary as egg composition varies. Thus, for my purposes, egg mass is not a good indicator of egg size.

For each egg component and treatment (supplemented or control), separate regressions were performed on 1984 and 1985 data. The only significant difference between years was found for lean yolk of eggs from food supplemented territories (Table IV-4). For all other components, the data were combined for the 2 years for presentation in Table IV-4 and for subsequent statistical comparisons. Results of comparable regressions for eggs from the farm habitat are also presented in Table IV-4, but only for reference as sample sizes were too small for statistical comparisons. Regressions on data from control and food supplemented territories were compared by seeing whether residuals were significantly lower when data were grouped by treatment than when data were treated as a single group; as a result, differences for slopes and/or intercepts were tested for simultaneously. The only significant differences occurred in water content, with dry albumin regressions also tending to differ. On average, albumin content was not affected by supplemental feeding (Table IV-4), but small eggs had less, and large eggs more albumin if they came from a food supplemented territory (Figure IV-1). The same pattern held for water content of eggs (Figure IV-2). The dry fractions of eggs from the farm habitat tended to resemble those from food supplemented territories, whereas for

Table IV-4: Statistics for allometric regressions of egg components on egg volume index. Data were a combined 1984-85 except for lean yolk mass of eggs from food supplemented territories, for which there was an annual difference between the regressions. Data for farm habitat clutches (an area of naturally higher reproductive success) are from 1984 alone and are included for comparative purposes but sample sizes preclude their use in statistical comparisons.

		Egg Source		
		Supplemented	Control	Farm
Dry Albumin:	b	1.44[2]	0.69[2]	1.47
	a	-6.29	-3.11	-6.48
	r^2	0.69	0.37	0.64
	n	18	16	5
Yolk Lipid:	b	0.54	1.25	0.72
	a	-2.74	-5.74	-3.47
	r^2	0.05	0.56	0.31
	n	18	16	5
		1984 1985		
Lean Yolk:	b	0.99[1] -1.06[12]	0.89[2]	0.57
	a	-4.76 4.00	-4.27	-2.92
	r^2	0.25 0.13	0.36	0.74
	n	8 10	16	5
Dry Shell:	b	0.88	0.71	0.86
	a	-4.01	-3.27	-3.89
	r^2	0.36	0.56	0.63
	n	18	16	5
Water:	b	1.09[1]	0.81[1]	0.83
	a	-3.77	-2.57	-2.65
	r^2	0.96	0.87	0.62
	n	17	16	5

[1]Regressions slopes and/or intercepts differed significantly at $P<0.05$.

[2]Regression slopes and/or intercepts differed at $0.10>P>0.05$.

Figure IV-1: Relationship between egg volume index (egg size) and dry albumin mass of black-billed magpie eggs from food supplemented and control territories.

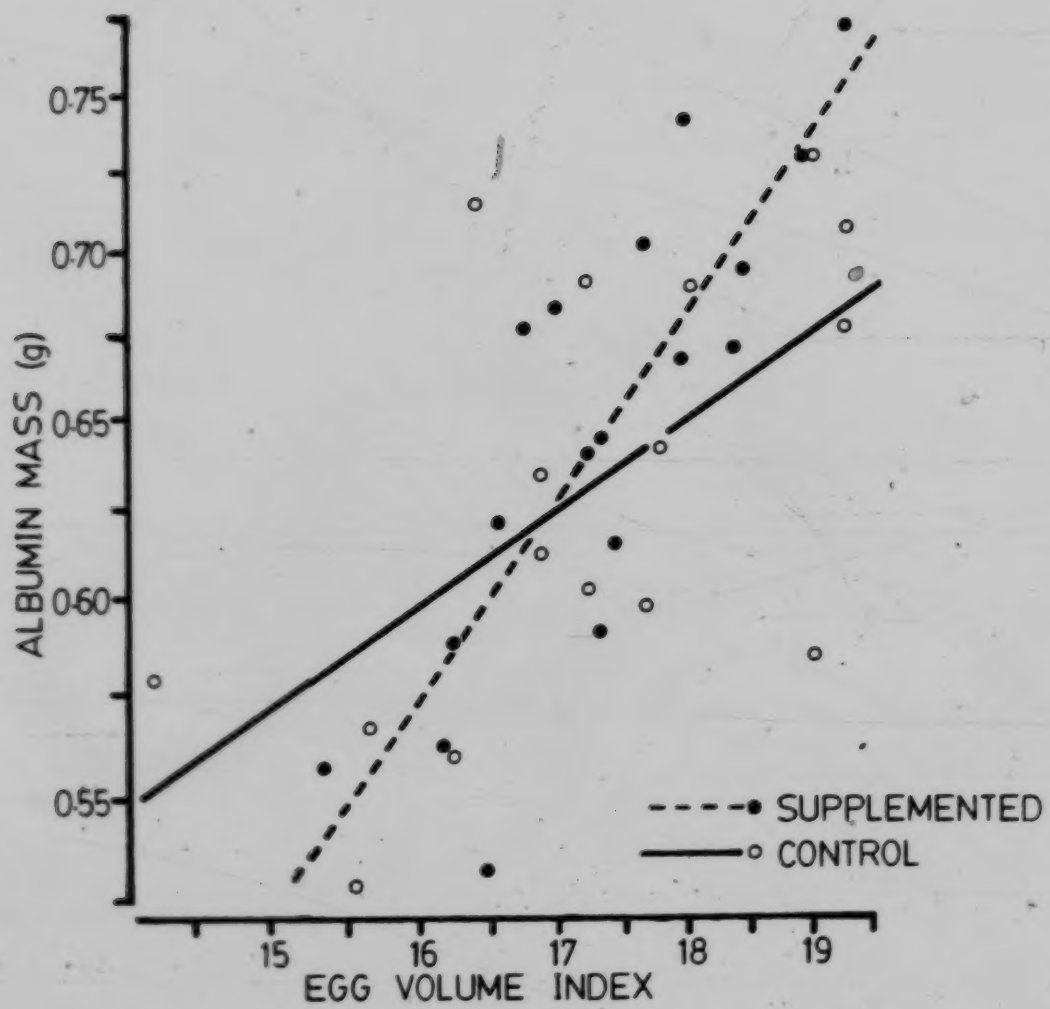
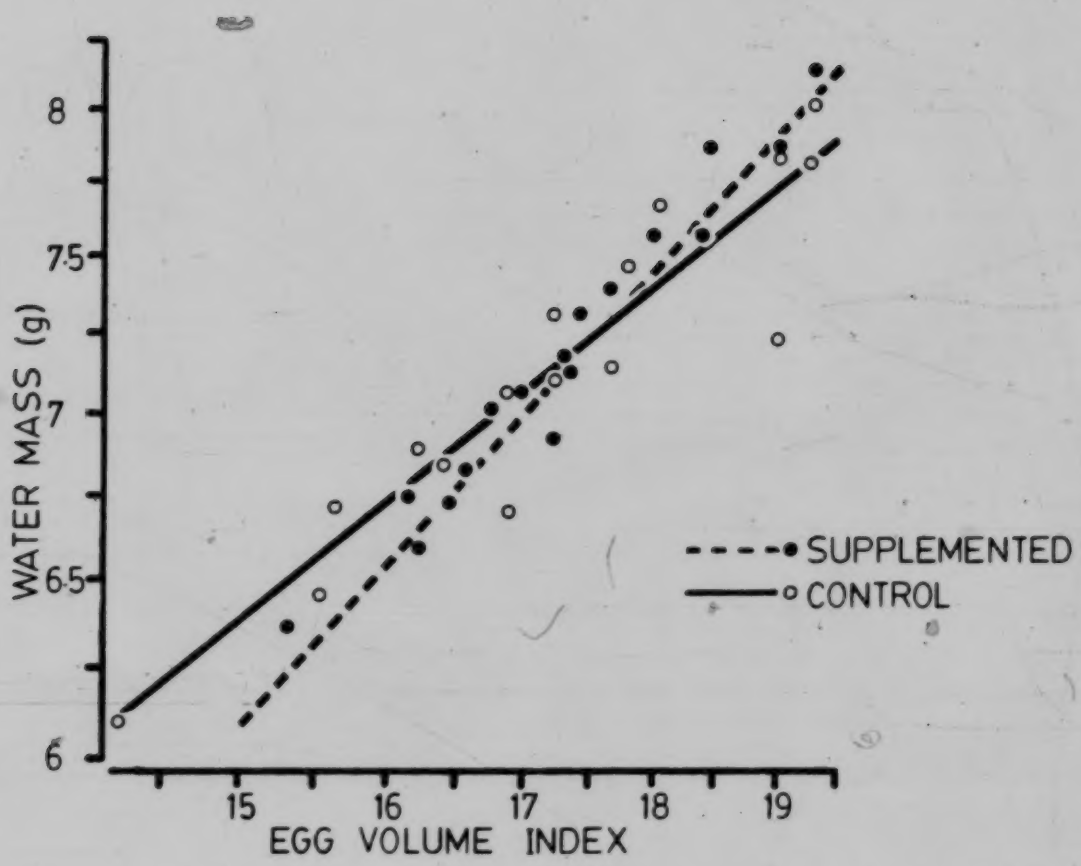


Figure IV-2: Relationship between egg volume index (egg size) and water content in blck-billed magpie eggs from supplemented and control territories.



water content of eggs from farm and control territories resembled each other more closely.

In summary, eggs from food supplemented territories did not have significantly greater masses of any egg component than eggs from control territories. However, the relationship between egg size and egg composition differed for eggs from food supplemented and control territories.

Variation in Egg Composition Within Clutches

Brood reduction (Ricklefs 1965) is often considered an important source of nestling mortality. Within nests, small eggs appear to pre-dispose chicks to die in cases where brood reduction occurs (*e.g.* Howe 1976). However, not only egg size, but also egg composition could vary within clutches so as to effect brood reduction (Howe 1978). Unfortunately, little is known about intra-clutch variation in egg composition. If lower rates of brood reduction for magpies in Edmonton were the cause of higher survival of nestlings on food supplemented territories, lower intra-clutch variation might be expected in clutches from food supplemented than control territories.

Intra-clutch variation in egg composition was first examined by comparing the variance within food supplemented and control clutches. Within clutch variance was calculated as the error mean-squared term of a one-way ANOVA among clutches, done separately for each egg component (Table IV-5). The percentage of variance occurring within clutches was calculated following the procedure of Sokal and Rohlf (1981). The only significant difference was a higher variance in shell mass within clutches from food supplemented territories. Lean yolk and yolk lipid were also more variable in food supplemented clutches, the differences bordering on significance.

Within clutch variation in egg composition was also examined with respect to egg size. Egg component masses were allometrically regressed on egg size, separately for each clutch for which at least 4 data points existed (Table IV-6). The collections of slope values from food supplemented and control clutches were used as data points in Mann-Whitney U-tests. Only for yolk lipid content did regression slopes differ between food supplemented and control clutches; slopes were lower with supplemental feeding. Thus, for a given range in egg size, there was less difference in lipid mass between the

Table IV-5: Within clutch variance (error mean square of one-way ANOVA among clutches) for eggs from food supplemented and control territories. CD (coefficient of determination) is the percentage of total variance occurring within clutches. Probabilities are for F-tests between supplemented and control clutch variances.

	Supplemented			Control			
	s^2	(df)	CD	s^2	(df)	CD	Probability
Dry Albumin (g)	2.4×10^{-1}	(39)	30.3%	1.6×10^{-1}	(40)	28.2%	$P=0.95$
Lean Yolk (g)	1.5×10^{-1}	(38)	60.7%	0.8×10^{-1}	(41)	64.2%	$P=0.06$
Yolk Lipid (g)	2.6×10^{-1}	(39)	45.0%	1.4×10^{-1}	(46)	62.7%	$P=0.06$
Shell (g)	4.2×10^{-1}	(42)	49.6%	0.8×10^{-1}	(46)	33.3%	$P<0.001$
Water (g)	1.1×10^{-1}	(32)	30.0%	1.2×10^{-1}	(40)	38.2%	$P>0.25$

TABLE IV-6: Median allometric regression slopes and coefficients of determination for intra-clutch regressions of egg components on egg volume index. Regression slopes from food supplemented and control territories were compared with Mann-Whitney U-tests (* denotes significant difference at $P<0.05$).

	Supplemented			Control		
	a	r^2	n	a	r^2	n
Dry Albumin	1.16	0.82	6	1.06	0.78	7
Lean Yolk	1.09	0.17	6	0.83	0.40	7
Yolk Lipid	0.83*	0.18	8	1.86*	0.50	8
Shell	0.71	0.51	7	0.53	0.43	8
Water	0.88	0.90	5	0.87	0.89	7

largest and smallest egg in clutches from food supplemented territories.

I did not compare intercepts from the regressions of within clutch composition on egg size. The point of the within clutch regressions was to examine the degree of variability in egg composition within clutches; regression slopes describe this variability (higher slope—greater difference between small and large egg). Intercepts have no biological meaning in this context.

In summary, egg composition was more variable in clutches from territories where supplemental food was present. What little systematic variation lipid content showed with egg size was at a lower rate in food supplemented than control clutches. Thus, when supplemental food was present there was less systematic disparity in lipid content of large and small eggs.

DISCUSSION

Comparison With Other Studies

To my knowledge, no other study has compared the composition of eggs of wild birds from areas known to differ in food availability. As a result, comparisons must be restricted to the patterns in egg composition found in single samples of eggs from different studies.

The biomass of egg components for a sample of 45 magpie eggs from Sheffield, England (Clarkson 1984) in comparison to eggs from this study are given in Table IV-7. The English magpie eggs were larger than those in Edmonton, with greater biomass of all components. However, shell masses were only marginally larger for British magpies, indicating that eggs from the British birds had thin shells relative to those collected in Edmonton.

The masses of egg components have been regressed on total egg mass for a number of species. Two general patterns in egg composition appear. First, water content of eggs (or wet albumin—the albumin being mostly water, and having the largest water store in the egg) was the component most highly correlated with egg mass (or volume, for the magpie eggs in the present study). This was true for northern gannet (*Sula bassanus*) (Ricklefs and Montevecchi 1979), laughing gull (*Larus atricilla*) and Japanese quail

Table IV-7: Size and composition [$\bar{x}$±s.d.,(n)] of black-billed magpie eggs from Sheffield, England and Edmonton, Canada. The sample from Sheffield is the mean of all eggs collected (with more than 1 egg from each nest), whereas the Edmonton sample values are the means of the mean values from all control clutches (1984 data only). Lipid masses may not be directly comparable as different solvents were used in the extraction process.

	Sheffield	Edmonton
Wet Albumin (g)	7.29±0.75 (45)	6.74±0.42 (7)
Dry Albumin (g)	0.74±0.11 (45)	0.64±0.07 (7)
Dry Yolk (g)	0.72±0.09 (45)	0.66±0.05 (7)
Lipid Mass (g)	0.55±0.06 (45)	0.36±0.03 (7)
Dry Shell (g)	0.58±0.06 (45)	0.54±0.04 (8)
Total Mass (g)	9.87±1.04 (45)	9.25±0.62 (8)
Volume Index (cm^3)	18.93±1.74 (45)	17.08±1.55 (17)

(*Coturnix japonica*) (Ricklefs *et al*. 1978) (correlations of shell mass on egg mass were not performed on eggs of the former 2 species), common tern (*Sterna hirundo*) (Nisbet 1978), magpies in England (Clarkson 1984) and Edmonton (Table IV-4), great tits (*Parus major*) and pied flycatchers (*Ficedula hypoleuca*) (Ojanen 1983), European starlings (*Sturnus vulgaris*) (Ricklefs 1984), boat-tailed grackle (*Quiscalus major*) (Bancroft 1985), and brown-headed cowbirds (*Molothrus ater*) (Ankney and Johnson 1985). I found no cases where this did not hold true. This is not surprising as eggs of precocial species are over 70% water and of altricial species over 80% water (Carey *et al*. 1980), so water mass and egg mass are relatively synonymous.

The second pattern is seen in yolk content of eggs. For almost all the studies noted above, lipid content or yolk size was the egg component most poorly correlated with egg size; a further study (Jones, *unpubl*., cited in Jones 1973) is consistent with the above pattern, finding no correlation between yolk size and egg size for red-billed quelea (*Quelea quelea*). The only exceptions were great tits (Ojanen 1983) and the control magpie eggs of magpies in the present study, but food supplemented and farm habitat magpie eggs followed the pattern of yolk lipid being the poorest correlate of egg size (Table IV-4). A poor correlation of yolk and egg size suggests that the physiological mechanisms determining yolk and egg size are relatively independent. Howe (1978) found that differences between the dry mass of eggs of different female common grackles (*Quiscalus quiscula*) were due almost completely to differences in yolk and not albumin mass. These results suggest that variation in yolk size (or the lipid content of the yolk) is an important facet of the total variation in egg composition. As yolk size is the egg component least likely to vary with egg size, if egg size is relatively unaffected by environmental factors, it is likely that yolk size variation linked to environmental change would not be detected in analyses concerned with egg size. Whether yolk size actually varied with territory quality (food supplemented *vs* unsupplemented territories) for magpies in Edmonton will be discussed below.

Variation in Magpie Egg Composition

As noted previously, the magpie eggs analysed in this study came from sources where different fledging success would be expected. Control (unsupplemented urban and

river valley habitat) clutches produced fewer fledglings than food supplemented (Table III-4) or farm habitat clutches (Chapter II). If fledging success is related to egg composition (Moss *et al*. 1975, Howe 1978), magpie eggs from different sources should vary in composition. Clutches from the food supplemented and farm territories should also be more similar to each other than to control clutches, because the former two groups both had relatively high fledging success.

Although differences were found among eggs from different sources (Table IV-3), eggs from food supplemented and farm habitat territories were not similar. In chapter II, I suggested that the tendency for higher fledging success on the farm habitat could be because eggs were larger there than elsewhere; yet, supplemental feeding did not influence egg size (Table IV-2). For the small samples where mean mass of egg components were known for clutches, control eggs tended to be intermediate to food supplemented and farm habitat eggs (Table IV-3). The only egg component to differ significantly among sources was yolk lipid, with smallest lipid masses in food supplemented eggs and largest reserves in farm habitat eggs. Thus, there is no indication that egg size (Figure II-3), or absolute mass of any egg component (Table IV-3, lack of similarity between food supplemented and farm eggs) had an over-riding influence on fledging success.

Examining the composition of average eggs from each nest may not be the most appropriate way to look for variation in egg composition. If egg size is highly heritable for magpies, as has been suggested for great tits (van Noordwijk *et al*. 1980), egg composition will be under constraints; larger yolked eggs may be advantageous, but if egg size cannot be changed an increase in yolk size would require a concomitant decrease in albumin or water content of the egg. This is the rationale for examining egg composition with respect to egg size, using allometric regressions (Table IV-4). Comparing regression statistics, food supplemented and farm habitat clutches resembled each other more closely than control clutches for dry albumin, yolk lipid, and shell mass. However, for the water content - egg size regressions, farm habitat eggs more closely resembled control eggs. These data suggest that the result of food supplementation may have been to affect the solids content of eggs so as to resemble eggs from the (presumably higher quality) farm habitat. Unfortunately, the small farm habitat sample precludes meaningful statistical

comparisons between eggs from all 3 sources.

When the larger samples from food supplemented and control territories were compared statistically, the only significant difference was for water content (Figure IV-2), with the difference in albumin content regressions approaching significance (Figure IV-1). With the provision of supplemental food, small eggs had proportionally less water than small control eggs; this relationship could also be viewed as small supplemented eggs containing proportionally more solids (lean and lipid fractions of yolk, and albumin). However, yolk and albumin appear not to vary in parallel: small eggs from food supplemented clutches had relatively little albumin (so that if total solids were greater than for control eggs, the yolks must have been relatively large), while larger food supplemented eggs had relatively large masses of albumin (implying small yolks, if the total solids content of these eggs was to be less than that of control eggs) (Figure IV-1).

The figures (IV-1 and IV-2) show that the degree of difference between food supplemented and control eggs was dependent on the size of the eggs produced. Thus, supplemental feeding may only have affected the quality of eggs within a certain size range. As egg size varied greatly among nests (Table IV-1), fledging success may only have increased on those territories where egg sizes fell within the range most advantageously affected by food supplementation. However, the above implies that some size classes of eggs are naturally of poorer quality, which was not the case as no relationship was found between egg size and fledging success (Figure II-3). Hence, I suggest that if supplemental feeding affected the average quality of eggs, the effect should have occurred for eggs of all sizes. I conclude that the changes observed in the composition of the average egg of a clutch with supplemental feeding were not advantageous in terms of fledgling productivity. Further, note that the differences among regression lines in Figures IV-1 and 2 may be due to one control clutch of very small eggs. Thus, differences among regression lines may be an artifact of the small samples available.

All comparisons made so far in the discussion have been based on mean values or single eggs from each clutch. The effects of supplemental feeding on variation within nests will now be considered. Both shell and yolk mass were more variable within food supplemented clutches (Table IV-5). However, only for lipid mass was the variation associated with egg size affected by supplemental feeding; supplemental feeding resulted

in a lower rate of change in lipid mass with egg size (Table IV-6).

Decreased rate of change in lipid content with egg size may have been adaptive for clutches on food supplemented territories. Egg size and hatchling size are correlated in a number of bird species (*e.g.* Schifferli 1973, de Steven 1978, O'Connor 1979, Ricklefs 1984b) including magpies (Clarkson 1984). If hatching asynchrony is eliminated, chicks from larger eggs may tend to survive better (Howe 1976), although this is not always the case (Schifferli 1973). The suggested cause for this differential mortality is brood reduction (Ricklefs 1965): smaller chicks (from small eggs) are killed by direct aggression (Braun and Hunt 1983) or from indirect competition with larger siblings for food. If brood reduction occurs for magpies breeding in Edmonton, and if this brood reduction is through indirect competition for parental feeding, clutches from food supplemented territories could produce more fledglings for the following reason. The lower slopes for lipid mass - egg size regressions of food supplemented clutches (Table IV-6) mean that for a given range in egg size there will be less difference in lipid content between smallest and largest egg in a clutch, relative to a control clutch with the same range in egg size. As well, the increased variablility in lipid mass within supplemented clutches (Table IV-5) suggests that there was less likelihood of the smallest egg also possessing the smallest yolk in the clutch. Thus, even if the smallest chick on a food supplemented territory had a relatively low food intake, a large lipid store could compensate, allowing the survival of the small chick over the first few days post-hatch (until all yolk lipid is exhausted). It is at or very near hatching that most mortality occurred in nestling magpies in Manchester, England (Tatner 1982), and if the same were true in Edmonton, the time of greatest mortality and the time at which yolk lipids are used would be the same. Even though lipid content of eggs tended to be more variable in food supplemented clutches (Table IV-5), the fact that this variability was independent of egg size could be adaptive.

Conclusions

Egg composition was influenced by supplemental feeding. Thus, it has been demonstrated that egg composition can be influenced by the type and / or amount of food available during the pre-laying period. A possible adaptive mechanism for the influence of egg composition on fledging success has been outlined above, but it is based on the

assumption that brood reduction is a significant source of mortality for nestling magpies in Edmonton. Eggs from food supplemented territories may have been of higher quality for other reasons; the analysis of egg composition was relatively crude and differences in egg quality may lie in the chemical composition and not the masses of egg components. It may well be that the effect of supplemental feeding was to "trick" laying females physiologically into into altering the composition of their eggs; but with this variation having no effect on fledging success. For instance, artificial advancement of clutch initiation could have caused early eggs in a clutch to have been produced by a reproductive system which was still not at its physiological optimum; this could increase variability in egg composition if egg composition were to change as the reproductive system developed. Hence, it has not been demonstrated that eggs produced on food supplemented territories were of higher quality than those on control territories. As noted in Chapter III, the effect of supplemental feeding may not have been to alter egg quality, but to improve the nutritional condition of the female.

Whether or not supplemental feeding increased egg quality, it has been shown that it may be necessary to consider egg quality with respect to egg size; if egg size cannot be varied, the potential quality of an egg can only be altered by changing the proportions of egg components. Furthermore, as egg composition varies both among and within clutches (*e.g.* Howe 1978), one cannot tell *a priori* that inter-clutch or intra-clutch variation is more significant in determining the quality of an egg. Clearly, for altricial birds it is necessary to consider egg quality as a product of both egg composition and size , and of composition of other eggs in the clutch.

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Chapter V

CONCLUDING DISCUSSION

In this thesis I have presented data on some attributes of magpie reproduction, including egg composition. I use this chapter to present some speculation which I considered inappropriate in the context of strict data interpretation. I consider the implications of my results, and point out research areas where more data are needed. Consequently, I view this chapter not as an end in itself, but as a starting point for further research.

When supplemental food was provided, magpies laid eggs which differed in composition from those on control territories (Tables IV-4 and IV-6). However, it was unclear whether this altered composition increased the likelihood that an egg would successfully produce a fledgling (increase egg quality). An alternative explaination for increased fledging success on territories with supplemental food (Table III-5) is that parental condition was improved, thus allowing the parents to successfully rear more young. Regardless of whether changes in egg composition represented an increase in egg quality on food supplemented territories, it is of interest to know which egg component(s) supplemental feeding directly affected. Because the total space inside an egg is limited, altering the mass of one component may require changes in the masses of other components; however, the mass of only one component need be directly affected by supplemental feeding. I provide a simplistic model of egg formation (based on the general sequence of events in egg formation, as outlined *e.g.* by Gilbert 1971a), and suggest at what points food supplementation was most likely to have affected egg composition directly. I start with two assumptions: (1.) the size of egg produced by a female is relatively fixed genetically (*e.g.* van Noordwijk *et al.* 1980) (which appeared to be the case with food supplementation, as supplemental feeding did not affect egg volume, Table IV-2), and thus an increase in the mass of one internal component would necessitate the decrease of other(s), and (2.), in the chronology of formation of egg components, the size of a component produced later cannot affect the size of a component already laid down.

The first egg component to form is the yolk (Gilbert 1971a). Either the nutrient composition of the yolk or its size could have been altered in birds provided with supplemental food. The only (crude) measure of yolk composition recorded was the ratio of lipid/non-lipid mass; this ratio was not altered by supplemental feeding (P=0.78, Mann-Whitney U-test). Yolk mass, however, was affected; yolk (especially the lipid

fraction) was more variable, and varied less systematically with egg size in clutches from territories on which supplemental food was provided (Table IV-6).

The second stage of egg formation is the secretion of albumin around the ovum (yolk) (Gilbert 1971a). Given a fixed egg volume, and a yolk already occupying part of that volume, the amount of albumin produced must be limited to that which fills the remainder of the egg. Hence, it appears that the volume of albumin is a function of yolk size, and differences in albumin mass with food supplementation (Table IV-4) were the result of the changes noted in yolk size. However, as water is still added to the albumin well after protein secretion ceases (Gilbert 1971b), the ratio of solids to water in the albumin may vary with changes in yolk size. The ratio dry albumin / albumin water mass was not a function of egg size, as regression between these two variables was not significant. However, a regression of dry albumin / albumin water mass against the dependent variable yolk solids / egg mass (the fraction of the egg occupied by the yolk) was significant (P=0.007, there was no difference between regression lines for eggs from food supplemented and control territories), and the slope was negative. Thus, as yolks occupied a larger fraction of the egg, the proportion of dry matter in the albumin decreased, meaning that an increase in yolk size resulted in either a decrease in the amount of solids or an increase in the amount of water secreted into the albumin (or both).

The shell is the last major component of the egg to be added. Shell thickness could have been affected on territories where supplemental food was present. Shell thickness can be described as the ratio of shell mass to egg size, or as a regression line of shell mass against egg volume. As I found that neither slope nor intercept of the shell mass-egg volume regression was altered by food supplementation (Table IV-4), shell thickness was not affected by supplemental feeding.

Thus, I conclude that food supplementation affected egg composition by altering yolk mass (and therefore volume), and that all other variation was due to this initial effect. This conclusion is based on the assumptions noted above, and since it is beyond the scope of this thesis to validate these assumptions, I do not pursue to question further. However, if my conclusion is valid, and if egg quality was increased on territories where supplemental food was provided, I suggest that the component directly affected (the yolk) is the one which most affected egg quality. Thus, when searching for mechanistic

explainations by which egg composition increased fledging success on food supplemented territories, variation in yolk size must be involved.

Besides egg composition, date of clutch initiation, clutch size, egg size, and parental size were examined with respect to their effects on fledging success. Date of clutch initiation was weakly correlated with fledging success (only about 5% of the total variance in fledging success could be accounted for by differences in laying date). Neither clutch size nor egg size (Figure II-3) was related to fledging success. As well, female and male size (Figures II-8 and II-9) did not affect fledging success. Clutch initiation (van Noordwijk *et al*. 1981), clutch size (*e.g.* Perrins and Jones 1974), and egg size (*e.g.* Ojanen *et al*. 1980, Moss and Watson 1982) have all been shown to be under some degree of genetic control. As none of these factors affected fledging success, there is no indication that genetic differences among females in reproductive parameters directly influenced reproductive success. Body size, which is also partially heritable (*e.g.* van Noordwijk *et al*. 1980), could potentially have influenced fledging success. For example, large males are dominant over small male magpies (Scharf 1985); if large (dominant) male magpies acquire better territories (Smith 1976, Reese and Kadlec 1984) there would be a correlation between male size and fledging success. This was not the case, and female size also was not correlated with fledging success. Thus, fledging success was not a function of any of the other reproductive parameters (which could be under genetic control) that were measured in this thesis.

That egg size did not affect fledging success (Figure II-3), and was not affected by supplemental feeding (Table IV-2) may be partially a function of the measure of egg size that I used; my size measure was an index of egg volume (length X breadth^2). Eggs of the same volume may differ in composition, as was shown in Chapter IV. As egg components have different densities, the overall density (and mass) of eggs will vary with their composition, even when egg volumes are the same. This may explain why Högstedt (1981) found supplemental feeding to affect "egg size" whereas I did not. Högstedt's (1981) measure of egg size was its mass, meaning that changes in either egg volume (with no change in density) or density (with no change in volume) could have been detected by him. However, I would only be able to detect changes in egg volume. Thus, I suggest that whenever egg size is being investigated, both egg mass and volume should be measured;

one could then determine whether the important characteristic of an egg was its size (volume), density (composition), or both. If egg volume is to a large degree under genetic control (*e.g.* Ojanen *et al.* 1979, van Noordwijk *et al.* 1980, Moss and Watson 1982), internal composition would be more likely to change than egg volume. Changes in egg density (and consequently in composition) without change in egg volume have been noted for shag (*Phalacrocorax aristotelis*) (Snow 1960), Canada geese (*Branta canadensis*) (Y. Leblanc, *pers. comm.*), and magpies (in the present study).

There was indication that extrinsic factors, in particular food availability (Table III-5) influenced fledging success. More specifically, the availability of food before the eggs hatched affected fledging success. Availability of supplemental food could have altered either egg quality, or the nutritional condition of the parents. I conclude that fledging success of magpies in Edmonton was mainly a function of survival of nestlings from hatching to fledging (not laying date or clutch size), and that survival was mediated by the supply of food available to the breeding pair before the eggs hatched. This is in sharp contrast to conventional wisdom, which suggests either that clutch size, or availablity of food after the young hatch are the two parameters critical to annual reproductive success (*e.g.* Lack 1966, Drent and Daan 1980). However, only McGillivray (1981) explicitly showed a close relationship between clutch size and fledging success.

The aim of my research was to determine what factors influenced annual fledgling production by black-billed magpies in Edmonton, and to look particularly at the ways in which food availability affected reproduction. My conclusions have been outlined above. My data not only provided conclusions, they also led to further questions; these questions are beyond the scope of this thesis to investigate. However, there are two topics on which I wish to speculate: (1.) whether variation in clutch size does affect parental reproductive success, but on a different spatial or temporal scale, and (2.) the potential ways in which behavior could influence parental reproductive success.

As clutch size had no effect on fledging success (Chapter II), there would be little reason to increase clutch size when breeding conditions are better than normal. This was the case, because clutch size did not increase among for birds with supplemental food on their territories (Chapter III). The number of fledglings was almost never (13 of 101

successful first nesting attempts, control and food supplemented territories combined) equal to the number of eggs in the nest. Given this situation, clutch sizes smaller than the observed should be selected for, if an egg represents a parental investment (using Trivers' 1972 definition of a parental investment being any investment in a given egg or offspring which prohibits the parent from investing in other offspring). That seemingly "extra" eggs were produced, suggests that the production of these eggs did not greatly affect the survival of the female, or her ability to incubate eggs or rear nestlings. However, even if there were little selection against larger than necessary clutches, there should be some advantage to producing the "extra" eggs. This selective advantage could take two forms. First, the advantage may be manifested only during those rare occasions when all eggs in a nest produce fledglings; in such cases; clutch size would produce an upper limit on fledging success. Second, the lack of correlation between clutch size and fledging success may be a very local phenomenon, restricted to the urban situation; immigration of magpies from outside this area (where most of the selection on clutch size could be occurring) could help maintain the high clutch size within Edmonton. Whatever the case, the data suggest that the heavy emphasis placed on the importance of clutch size as a determinant of fledging success (*e.g.* Lack 1966, Drent and Daan 1980) may be misdirected in some instances.

Behavioural differences between magpies, which were not examined in this thesis, could have affected survival of nestlings, and post-fledging young. A potential behavioural difference is in foraging ability. Differences could exist in the rate at which food was obtained by the female (through her own foraging, or courtship feeding by the male), or in the rate that parents fed their young. The latter seems unlikely, as there was no apparent shortage of food at the time nestlings were being fed (supplemental feeding initiated after egg laying did not affect fledging success, Table III-3). If differences existed in foraging ability, the mechanism by which reproduction was affected would not differ from that in which there were variation in the availability of food among territories. Another behavioural effect could be manifested through social dominance. It has already been shown that dominant male magpies in Edmonton did not acquire better territories (Figure II-7), contrary to the suggestions of Smith (1976), and Reese and Kadlec (1984). However, the advantage of parental dominance may appear only after the young have reached

independence. If body size of magpies is heritable, male offspring of large parents will be relatively dominant, which could affect their chance of over-winter survival (Scharf 1985). If dominance is heritable independent of body size (as for Japanese quail (*Coturnix japonica*), Boag and Alway 1981, Boag 1982), overwinter survival of females could also be affected by parental dominance (there was no correlation between female size and dominance (Scharf 1985)).

In summary, it is not known whether egg composition, in particular variation in yolk size, affected chick survival, either by reducing the rate of brood reduction or for some other reason, or whether the nutrition of laying or incubating females affected their behaviour so as to vary fledgling production among territories. For instance, did females in poorer nutritional condition spend less time incubating eggs or brooding nestlings? Also, it was unknown whether variation in food availability would be due to variation in food supply among territories, or in foraging ability of birds, or both. Ultimately, however, it must be shown whether the variation in reproduction in single breeding seasons described in this thesis had any effect on the fitness of breeding black-billed magpies. These questions are for further research. It is clear, however, that within a single breeding season fledgling production was related more to environmental parameters such as food availability, than to intrinsic factors like clutch size or egg size. Further, my data suggest that the time at which food availability had its greatest effect on fledgling was around egg formation. Together, these conclusions have never been found in any other study on wild birds.

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